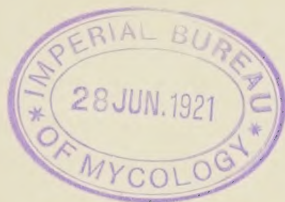


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SCHOOL OF AGRICULTURE

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Adams, J. F.
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I. RUSTS ON CONIFERS IN PENNSYLVANIA

II. SEXUAL FUSIONS AND DEVELOPMENT OF
THE SEXUAL ORGANS IN THE
PERIDERMIIUMS

STATE COLLEGE, CENTRE COUNTY, PENNSYLVANIA

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I. RUSTS ON CONIFERS IN PENNSYLVANIA*

J. F. Adams

Among the diseases of a parasitic origin attacking the conifers, a large number belong to a group commonly called the rusts. The rusts make up a specialized group of parasitic fungi that are common and widely distributed. While some of the common rusts such as attack the cereals, asparagus, blackberry, hollyhock and apple are familiar to many, the rusts on the conifers are not so generally known.

The rusts which are considered here are of economic importance in several instances as nursery diseases where many of the stem forms often kill the seedlings. In forest plantations and pine stands they are often destructive. It is not uncommon to find trees killed outright by the girdling effect of some stem rusts. In many instances the trees are so weakened that they are blown over by the wind or broken down by the snow. Conifers used as ornamentals are often dwarfed or unsightly from the attack of certain stem and leaf rusts. One of the most important pine rusts, commonly known as the White Pine Blister Rust, has become established in this country through importations of five-needle pines from Europe. This disease is so well established in some of the New England states that the planting of white pine has now been abandoned.

The blister rusts on the pines have been a departmental project since 1914 under the leadership of F. D. Kern, C. R. Orton and the writer.

Among the earliest collections of rusts on coniferous hosts in Pennsylvania are those found in the collections of fungi by Schweinitz, made during his residence in this country between 1812 and 1834. His collections were mostly from the vicinity of Bethlehem, except for a few around Philadelphia. Arthur and Bisby⁽¹⁾ have recently studied and listed the rusts of North America recorded by Schweinitz. In this list are found five genera representing eleven species of coniferous rusts occurring on conifers or their alternate hosts. These represent several species and hosts which are not present in our collection for the state.

In 1914 Orton and the writer⁽²⁾ published an article entitled "Notes on *Peridermium* from Pennsylvania". No previous account of these

*Contribution from the Department of Botany, The Pennsylvania State College, No. 20.

1. Arthur, J. C., and Bisby, G. R., An Annotated Translation of the Part of Schweinitz's Two Papers giving the Rusts of North America. Proc. Am. Phil. Soc. Vol. LVII, 1918.

2. Orton, C. R., and Adams, J. F., Notes on *Peridermium* from Pennsylvania. Phytopathology 4, 23-26, 1914.

rusts had been published for Pennsylvania. This present report is the result of observations and collections made in various parts of the state, but for the greater part in the vicinity of State College. In spite of this fact it is believed the species reported give an accurate idea of the representative coniferous rusts of this state. Further observations in the state no doubt will reveal a wider distribution of these species and perhaps identify the alternate stages for those species whose complete life cycle is not known.

In appearance the rusts can usually be recognized by the powdery appearance of their fruiting or spore stages, which are white, yellow, orange, red, or black in color. This color is imparted by the spores which are borne in definite groups called sori. These vary in shape and size, usually embedded, but sometimes elevated above the surface of the host tissue. The sori on leaves usually appear on yellow or discolored spots. They also may be observed on the stems as swellings or galls. Depending on the type of sori in which the spores are formed they are known as the *pycnium* (O), *aecium* (I), *uredinium* (II), and *telium* (III)⁽³⁾.

With the rusts on conifers the pycnial and aecial stages are usually associated together. The uredinial and telial stages are generally found on an alternate host. Little is known as to the function of the pycnial stage, but the other three stages are known to be reproductive. The aecium is the most conspicuous stage, where the spore mass is covered with a whitish receptacle called the peridium. In some species the peridium is absent and this stage is then called a caeoma.

These rusts of conifers with three or four stages present a complicated life history since they usually spend their life cycle on two separate hosts. The condition where two different plants are required to complete the full life cycle of a rust is known as heteroecism. This interesting situation was first discovered and proved with the stem rust of wheat, when it was found that the aeciospores developed on the leaves of the barberry could infect the wheat, producing first the uredinial or red rust stage and then the telial or black rust stage. The teliospores formed on the wheat were found to winter over and in the following spring to germinate, producing secondary spores (sporidia) which were capable of infecting the barberry and thus completing the life cycle.

3. This terminology with respect to the various spore stages of the rusts follows that used by Dr. Arthur in his monograph of the *Uredinales* in the North American Flora. The older terminology was used in the preparation of the manuscript for the second part and has been retained in publication.

The first group of rusts which is considered in this report occurs on pine, hemlock, fir, spruce and larch and belongs to the two form genera *Peridermium* and *Caeoma*. The species of the rusts belonging to the genus *Peridermium* were reported by Arthur and Kern in 1906 as represented in this country by twenty-seven species, only three of which had been definitely associated with their alternate hosts. Since that time numerous reports of connections and additional species have been made, so that now about twice that number are known to be established in this country. So far we have found thirteen species established in this state of which the full life cycle is known. There are also six species of rusts of which only the uredinial and telial stages are known, but which are known to have for their alternate stage a *Peridermium* or *Caeoma*. When the peridermial stage is known the rust then takes the name of the genus on the telial host.

The aecia of the form genus *Peridermium* are usually quite conspicuous as cylindrical or blister-like outgrowths occurring upon the stems (caulicolous) or upon the needles (follicolous). When the aeciospores are liberated from the aecium, and conditions are favorable for their germination on the alternate host, the fungus then becomes established and develops the uredinial stage. The urediniospores are formed which are only capable of repeating the infection upon the same host. Later on the uredinial stage is followed by the development of the telial or winter spore stage. The teliospores germinate in the fall or following spring and produce secondary spores (sporidia) which are wind disseminated and infect the coniferous host. Following infection on the coniferous host the pycnial stage develops and then the aecial stage. Thus the life history of these heteroecious rusts is completed.

The second group of rusts considered belongs to the genus *Gymnosporangium*. This genus is characterized by the development of the pycnial and aecial stages (with the exception of three species) on the leaves and fruit of different rosaceous hosts such as the apple, quince and hawthorns. The aecia appear as cylindrical outgrowths or as cluster-cup developments. The uredinial stage is lacking in this genus with one exception. The telial stage is restricted to the different species of cedars. The telial stage on the cedars when mature often appears as an orange or rusty gelatinous mass of spores. These cedar apples are a familiar sight to many in the spring. Telia occur upon the stems and in some species upon the leaves of cedars.

The destructive effect of many of these rusts may be obviated by removing one of the alternate hosts. Consideration should be given to prevent the planting of alternate hosts together for ornamental purposes. It is hoped in reporting the forms established in this state to arouse more interest in their importance and distribution as well as to assist in determining the alternate hosts of those not yet known.

Dr. G. G. Hedgcock of the Bureau of Plant Industry, office of Forest Pathology, has kindly supplied the data for numerous collections, particularly those made by himself.

Photographs illustrating the various species of rusts were available through the kindness of Dr. L. O. Overholts (Figs. 5 and 6), Dr. A. S. Rhoads (Figs. 2 and 9A), and Mr. E. T. Kirk (Figs. 1, 3, 4, 7, 9C, 10).

1. *PERIDERMIIUM COMPTONIAE* (Arthur), Orton and Adams, *Phytopath.* 4:24, 1914.

(*Cronartium Comptoniae* Arthur)

The first report of this species of *Peridermium* in Pennsylvania is a collection by W. A. Buckhout on *Pinus rigida* in Centre County, Penna., June 1, 1891. A. R. Gerhart, a forestry student of The Pennsylvania State College, collected this species on *Pinus rigida* near Bear Meadows, Centre County, Penn'a, May 26, 1913. Since these early collections additional specimens have been collected at various times by different members of the Botany Department.

The type of infection varies in appearance upon the different species of pine, but has been found always confined to the trunk or lower branches near the ground.

Kern and the writer investigated an outbreak of this rust on the Jacob Nolde estate near Reading, Penna., July 4, 1914, where it was established on the Bull Pine, *Pinus ponderosa*, growing in a nursery. The trees were about five years old and the infection was characterized by a slight, fusiform swelling just above the surface of the ground and extending up to the lowermost branches. Within fifty feet of these infected pines in a cut over area was a dense growth of sweet fern (*Comptonia asplenifolia*) which showed abundant uredinial infection on the leaves. Further observation of infection on the Bull Pine was made by the writer at Stone Valley, Huntingdon County, Penna., May 12, 1917. In a planting of about 150 Bull Pines, nine were found infected. The infection was restricted near the ground level and always below the region

of branching. The pines were about five years old, having been transplanted when three years of age.

Infection on pitch pine (*Pinus rigida*) collected at Bear Meadows, Centre County, Penna., has shown an extended area of infection, with aecia appearing at irregular intervals for a distance of twelve inches and more on the trunk. This may be an incipient infection which eventually would develop into the spindle gall form. The trees concerned showed a spindling growth and were about seven years of age.

In this vicinity the most characteristic infection is found on our native pine, *Pinus virginiana*. Infection is found on trees of various ages and while usually restricted to the trunk it is not uncommon to find it on the lower branches. The infection appears as irregular semi-globoid swellings which are usually rough in appearance with the old bark adhering as shown in Figure 1. On the trunk the infection may appear as an aggregate mass of distinct galls, sometimes restricted to one side but often found girdling the trunk. In some instances infection has girdled the branches resulting in a typical globoid gall very similar to certain types of infection by *Peridermium cerebrum*. This type of gall has also been observed by the writer on the same host at Lakehurst, New Jersey. Additional infection of this type has been forwarded by C. A. Schwarze on *Pinus rigida*, Admiral, Md., June 9 and 10, 1919.

This rust appears to be quite destructive to young pines. In some instances young trees have been observed to be killed outright where the trunk was girdled. Frequently the young trees are stunted or dwarfed in their growth.

Mature aecia have been observed in the field as early as May 10 and often up to the last of July. The fungus is perennial in the host and is most abundant in the cortical tissue. When the aecia are sporulating the infection is conspicuous with the orange colored spore mass. The peridium is very characteristic with a tooth-like margin along its dehiscence.

Orton has cultured the various forms collected on the pines. Aeciospores from the fusiform swelling on *Pinus rigida* collected at Bear Meadows were sown in greenhouse on Sweet Fern (*Comptonia asplenifolia*) June 3, 1914, with uredinia appearing June 25, 1914. Three species of oaks were used as checks and these showed no infection. The gall form on *Pinus virginiana* collected at Charter Oak was cultured in greenhouse on Sweet Fern, May 12, 1918, with mature uredinia appear-

ing May 22, 1918. The gall form on *Pinus rigida* from Admiral, Md., was cultured on Sweet Fern, June 9 and 10, with uredinia appearing June 18, 1919.

O and *I*. Caulicolous.

Pinus rigida Mill., Centre Co., June, 1891, W. A. Buckhout; Bear Meadows, Centre Co., May 26, 1913, A. R. Gerhart, May 24, 1914, C. R. Orton, A. S. Rhoads and J. F. Adams.



Fig. 1. *Peridermium Comptoniae* on *Pinus virginiana* showing the irregular semi-globoid swellings. These were taken from infection on the trunk of young trees. The specimen on the right shows infection on two of the lower branches.

Pinus ponderosa Dougl., Mohnton, Berks Co., July 4, 1914, *F. D. Kern* and *J. F. Adams*; Stone Valley, Huntingdon Co., May 12, 1917, *J. F. Adams*; Colemanville, Lancaster Co., July 26, 1910, *J. F. Collins*.

Pinus virginiana Mill., Stone Valley, Huntingdon Co., July 31, 1914, *C. R. Orton*, *J. B. Demaree* and *A. S. Rhoads*; June 10, 1915, *C.*



Fig. 2. *Peridermium pyriforme* on *Pinus pungens*. This photograph was taken of the tree in the field. The infection is restricted to the lower part of the trunk near the ground level and shows a slight fusiform swelling. At this time the aecia were erumpent.

R. Orton and J. F. Adams; May 12, 1917, L. O. Overholts, G. A. Meckstroth and J. F. Adams; May 12, 1919, L. O. Overholts; Charter Oak, Huntingdon Co., May 21, 1916, C. R. Orton and L. O. Overholts; May 10, 1918, C. R. Orton.

Pinus pungens Lamb., Greenwood, Huntingdon Co., May 31, 1917, J. O. Bietsch.

Pinus densiflora Siebold; Conococheague Creek, Adams Co., May 25, 1914, J. S. Illick and G. G. Hedgcock.

Pinus nigra Hoss., Conococheague Creek, Adams Co., May 25, 1914, G. G. Hedgcock.

2. *PERIDERMIIUM PYRIFORME* Peck, Bull Torrey Club 6:13, 1875.

(*Cronartium pyriforme* (Peck) Hedgcock and Long).

The first collection in the state of this *Peridermium* was made by C. R. Orton and the writer on *Pinus pungens* at Charter Oak, Huntingdon County, Penna., June 2, 1913. It has been observed so far only on this pine in Huntingdon County.

Infection is found on the trunks close to the ground and occasionally including the lowermost branches, Figure 2. The infection may be easily overlooked even when the fungus is sporulating. On this species of pine practically no hypertrophy of the trunk is evident. However, this same species of *Peridermium* is known to cause a fusiform or globoid swelling on other two and three-needle pines. The aecia have been observed sporulating as early as May 20. The peridium does not persist, as with the previous species, and appears to be evanescent.

The alternate stage occurs on Bastard Toadflax (*Commandra umbellata*). It was collected in the field at Charter Oak, August 31, 1913, by F. D. Kern, C. R. Orton and J. B. Demaree, when it was first reported to be associated with this *Peridermium*.

Infection on *Pinus ponderosa* was produced by Orton and the writer in 1915, Figure 3. Leaves of *Commandra umbellata* with mature telia were collected at Charter Oak and this material was used for inoculation on Bull Pine at State College, September 1, 1913. The culture was not observed in 1914, but August 1, 1915, the tree was severely infected with the rust. It is not certain that the aecia did not appear in 1914, yet it is our belief that it requires two years for it to become established and sporulate.

O and I. Caulicolous.

Pinus pungens Lamb., Charter Oak, Huntingdon Co., June 2, 1913, C. R. Orton and J. F. Adams; May 17, 1914, F. D. Kern and J. F. Adams; June 31, 1914, C. R. Orton and J. F. Adams; May 20, 1917, J. F. Adams; Greenwood Furnace, Huntingdon

Co., May 28, 1914, G. G. Hedgcock; Petersburg, Huntingdon
Co., June 3, 1914, G. G. Hedgcock.



Fig. 3. *Peridermium pyrifforme* on *Pinus ponderosa* showing a fasten on the trunk of the trunk. This is an infection produced on a five year old pine.



Fig. 4. *Peridermium cerebrum* on *Pinus rigida* showing fusiform type of infection. The aecia have not ruptured and appear as the white blister developments.

3. *PERIDERMIIUM CEREBRUM*, Peck, Bull. Buffalo Soc. Nat. Sci. 1:68, 1873.

(*Cronartium cerebrum* (Peck), Hedgcock and Long).

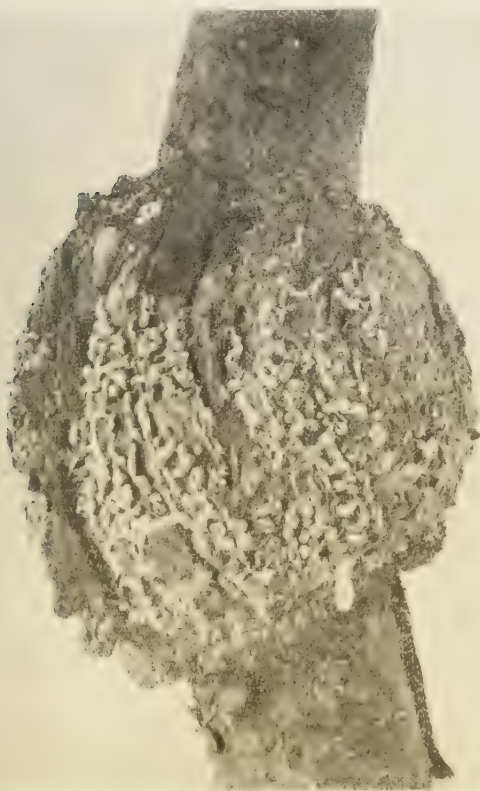


FIG. 5. *Peridermium cerebrum* on *Pinus virginiana*. A typical globoid gall. Not all of the aecia have ruptured as shown by the white blister developments.

This rust appears in various forms of distortion on the different two and three-needle species of pine. So far it has not been observed to be very prevalent in this vicinity. Infection on young trees of *Pinus rigida* appears as a fusiform enlargement as shown in Figure 4. Dr. Kern has

collected the typical globoid type of infection on *Pinus virginiana* at Charter Oak, Figure 5.

The alternate stage is found on different species of oak. As with other stem forms, the mycelium is perennial on the pine.

The aecia before dehiscence appear similar to *P. Comptoniae* but the peridia do not rupture with the tooth-like margin of this species. The peridium is not so persistent after the aecia are mature. These have a typical circumscissile dehiscence.

The fusiform type of infection collected on *Pinus rigida* has been cultured on *Quercus alba* by Orton. Aecia were sown in the greenhouse on white oak seedlings May 29, 1914, uredinia being observed June 20, 1914.

O and I. Caulicolous.

Pinus rigida Mill., Charter Oak, Huntingdon Co., May 13, 1913, E. T. Kirk and D. C. Babcock; Bear Meadows, Centre Co., May 24, 1914, C. R. Orton; Mt. Alto Park, Franklin Co., May 25, 1914, G. G. Hedgcock; Conococheague Creek, Adams Co., June 1, 1915, G. G. Hedgcock.

Pinus virginiana Mill., Charter Oak, Huntingdon Co., May 21, 1916, F. D. Kern; Philadelphia (vicinity), L. D. Schweinitz (2903); Old Forge, Franklin Co., May 25, 1914, G. G. Hedgcock; Peru Mills, Juniata Co., June 2, 1914, G. G. Hedgcock; Mt. Alto, Franklin Co., September 4, 1914, G. G. Hedgcock.

4. PERIDERMIIUM STROBI Kleb. Abh. Nat. Ver. Bremen. 10:153, 1887.
(*Cronartium ribicola* Fischer).

This is the most destructive blister rust that is known to occur in this country. It is permanently established in the New England states, and common throughout Europe. The disease has been introduced into this country through the importations of European nursery stock. So far in Pennsylvania it has appeared only as a nursery infection. The white pine as well as other species of five-needle pines are subject to this disease.

In some sections of the New England states it has proved so destructive to the white pine that their planting is for the present abandoned. As with the other stem rusts of pines, the mycelium is perennial but is more active and destructive. The alternate stage is known to occur on various species of currants and gooseberries (*Ribes* spp.).

Our knowledge of the distribution of this rust has been augmented through the kindness of R. G. Pierce of the Forest Pathology Office, Bureau of Plant Industry, Washington, D. C.; S. B. Detwiler, of the

United States Department of Agriculture, and J. G. Sanders, of the State Bureau of Plant Industry, Harrisburg, Penna.

O and I. Caulicolous.

Pinus strobus L., Chestnut Hill, Philadelphia, at the Andorra Nursery. Mr. Francis Windle, a state nursery inspector, states that the blister rust was found first either in 1910 or 1911, then in 1912, 1913, 1914, and 1916. Twenty thousand trees of *Pinus strobus* had been imported in 1907 from J. Heins of Halstenbek, Germany; Johnstown, Cambria Co., October 19, 1916, at the Cambria Mining and Manufacturing Company. Mr. J. G. Sanders found the infection on trees from the American Forestry Company of South Framingham, Mass.; Delaware Water Gap, Monroe Co., July 27, 1910, J. F. Collins. This infection was collected on the grounds of D. D. Drake. Between 1903 and 1910 there had been imported nearly half a million white pines. Four hundred thousand trees of this importation were



Fig. 6. *Peridermium Strobi* on *Pinus strobus*. Showing typical erumpent aecia on branch and trunk infection.

from J. Heins, of Halstenbek, Germany, and the others from Orleans, France; Bryn Mawr, Montgomery Co., March 3, 1910, *Perley Spaulding*. This infection was collected at the place of G. H. Earle, Jr., who had imported about one thousand white pines from Europe; Reading, Berks Co., October 19, 1916, *M. F. Barrus* on the "Sheerlund" estate of D. D. Horst; Reading, Berks Co., 1915, *P. Spaulding*, and October 24, 1916, *M. F. Barrus*. These infections were collected on the estate of Jacob Nolde, who had imported thousands of white pines from J. Heins, of Halstenbek, Germany; Morrisville, Bucks Co., 1909, *J. F. Collins*. Mount Union, Huntingdon Co., 1915, *R. G. Pierce*. These two infections were from the nursery and plantations of the Pennsylvania Railroad at Morrisville and Mt. Union. In 1908 the Pennsylvania Railroad imported thousands of white pines from J. Heins and other European nurseries. These pines were planted in the nursery at Morrisville or in various plantations at Elizabeth Furnace, Kinzer, Leaman Place, Lewistown Junction, Martin Forge, Mt. Union and Pomeroy, Pennsylvania.

5. *PERIDERMIIUM ACICOLUM* Underwood and Earle. Bull Torrey Club 23: 400, 1896.

(*Coleosporium solidaginis* (Schw.) Thuem.).

This is one of our most common needle forms of rusts on the two and three-needle pines. Infection on leaves may be recognized as early as March as distinct pale yellow bands varying in length from 2 to 5 mm. The aecia are conspicuous on pale yellow spots and usually appear during the month of June in this vicinity. The *II* and *III* are most commonly found on various species of *Aster* and *Solidago* with one collection on *Callistephus hortensis*.

(*O*) and *I*. Follicolous.

Pinus rigida Mill., State College, June 31, 1891, *W. A. Buckhout*; Bear Meadows, Centre Co., June 13, 1913, *C. R. Orton* and *J. B. Berry*; Pine Grove Mills, Centre Co., June 1, 1914, *C. R. Orton*, *J. B. Demaree* and *J. F. Adams*; Mt. Alto Park, Franklin Co., May 20, 1913, *G. G. Hedgcock*; Conococheague Creek, Adams Co., *J. S. Illick* and *G. G. Hedgcock*, May 25, 1914; Rothrock Run, Juniata Co., May 28, 1914, *G. G. Hedgcock*.

Pinus pungens Lamb., Charter Oak, Huntingdon Co., June 31, 1913, *C. R. Orton* and *J. F. Adams*; May 31, 1914, *F. D. Kern* and *J. F. Adams*; Mt. Alto Park, Franklin Co., May 24, 1914, *G. G. Hedgcock*; Belleville, Mifflin Co., May 29, 1915, *G. G. Hedgcock*.

Pinus echinata Mill., Mt. Alto Park, Franklin Co., May 24, 1914, *G. G. Hedgcock*; Mt. Alto Park, Adams Co., June 1, 1915, *G. G. Hedgcock*.

Pinus resinosa Att., Conococheague Creek, Adams Co., June 1, 1915, *G. G. Hedgcock*.

Pinus nigra (Hoss.) var. *Austriaca* Endl., Conococheague Creek, Adams Co., June 2, 1916, *G. G. Hedgcock*.

Pinus nigra Hoss., Conococheague Creek, Adams Co., June 2, 1916,
G. G. Hedgecock.

6. PERIDERMIIUM DELICATULUM Arthur and Kern, Bull Torrey Club
33:412, 1906.

(*Coleosporium delicatulum* (Arthur and Kern) Hedgecock and
Long).

This species is known to occur on the two and three-leaf pines. The
aecia are very much reduced in comparison with *P. acicolum* and for
this reason with such inconspicuous peridia may be easily overlooked.
The uredinia and telia are commonly found on Flat-topped Goldenrod,
Euthamia graminifolia.

O and I. Follicolous.

Pinus rigida Mill., Mt. Alto Park, Franklin Co., May 25, 1914, G.
G. Hedgecock; Old Forge, Franklin Co., May 25, 1914, G. G.
Hedgecock; Greenwood Furnace, Huntingdon Co., May 27, 1914,
G. G. Hedgecock; Cross Keys, Juniata Co., June 1, 1914; G. G.
Hedgecock.

Pinus echinata Mill., Mt. Alto, Franklin Co., June 1, 1915, G. G.
Hedgecock.

Pinus nigra Hoss., Conococheague Creek, Adams Co., May 25, 1914,
G. G. Hedgecock.

7. PERIDERMIIUM CARNEUM (Base.) Seym. and Earle, Econ. Fungi
550, 1899.

(*Coleosporium Vernoniae* B and C.).

The aecia occur on two and three-leaf pines. They are very con-
spicuous and much larger than *P. acicolum*. The uredinia and telia occur
on various species of *Vernonia*, but so far we have collected it on but
one species, *V. noveboracensis*. It is reported to live over winter in the
uredinial stage on the rosettes of *Vernonia*.

O and I. Follicolous.

Pinus rigida Mill., Conococheague Creek, Adams Co., June 1, 1915,
G. G. Hedgecock.

8. PERIDERMIIUM HELIANTHI (Schw.) Hedgecock and Hunt. Myco-
logia 9:240, 1917.

(*Coleosporium Helianthi* (Schw.) Arthur).

Dr. Hedgecock has made several collections of this rust in Hunting-
don County. The uredinia and telia occur on *Helianthus* and have been
collected on the following species: *H. strumosus*, *H. tuberosus*, *H. de-
capetalus*, *H. divaricatus* and *H. giganteus*.

O and *I*. Foliicolous.

Pinus virginiana Mill., Greenwood Furnace, Huntingdon Co., May 27, 1914, May 29, 1915, May 31, 1916, *G. G. Hedgcock*.

9. PERIDERMIIUM IPOMOEAE (Schw.) Hedgcock and Hunt, Mycologia 9:239, 1917.

(*Coleosporium Ipomoeae* (Schw.) Burrill).

The aecia occur on the needles of two and three-leaf pines. Dr. Hedgcock has made the only collection of aecia in this state. Only two collections of the alternate stage on *Ipomea* spp. have been made.

O and *I*. Foliicolous.

Pinus rigida Mill., Mt. Alto, Franklin Co., June 1, 1915, *G. G. Hedgcock*.

Pinus echinata Mill., Mt. Alto, Franklin Co., June 1, 1915, June 1, 1916, *G. G. Hedgcock*.

10. PERIDERMIIUM PECKII Thuem. Mitth. Forstl. Vers. Oest. 2:320 (24), 1880.

(*Pucciniastrum myrtilli* (Schum.) Arthur).

This needle rust is very common on the hemlock in Centre and Huntingdon Counties. The infected leaves of the new growth are pale yellow with the cylindrical aecia appearing on the under surface in two parallel rows. In 1917 mature aecia were observed May 20th while in 1919 they were not mature until the latter part of June. Regardless of the early spring in 1919 the new growth on the hemlocks was later in appearing than in 1917. Arthur has reported two distinct species of *Pucciniastrum* on vacciniaceous hosts in the North American Flora, *P. myrtilli* and *P. minimum*. The writer and C. R. Orton have cultured *Peridermium Peckii* on *Azalea nudiflora*, *Vaccinium angustifolium* and *Gaylussacia* spp. Aeciospores were sown in the field July 20, 1914, on these hosts and mature uredinia were observed July 29, 1914. Field evidence supported by cultures indicates the relationship between *Pucciniastrum minimum* and *P. myrtilli* and are such that they may be identical.

O and *I*. Foliicolous.

Tsuga canadensis (L.) Corr., Charter Oak, Huntingdon County, August 17, 1914, *C. R. Orton*; July 19, 1914, *C. R. Orton* and *J. F. Adams*; July 8, 1916, *C. R. Orton*. Bear Meadows, Centre Co., July 8, 1916, *C. R. Orton* and *L. O. Overholts*; Shingle-town Gap, July 4, 1916, *C. R. Orton* and *J. P. Kelly*.

11. *PERIDERMIIUM HYDRANGEAE* (B. and C.) Adams, Mycologia
12: 1920.

(*Pucciniastrum Hydrangeae* (B. and C.) Arthur).

The alternate stage of this *Peridermium* was collected for the first time on *Hydrangeae arborescens* in 1917. In the spring of 1919 the writer made a visit to the same vicinity and collected a *Peridermium* on



FIG. 7. *Caeoma abietis canadensis* on the cones of *Tsuga canadensis*. Infection involves the entire cone. When the caecoma have ruptured the cone is changed to a bright orange imparted by the spores.

hemlocks resembling the form of *P. Peckii*. This *Peridermium* was successfully cultured in the greenhouse on *Hydrangeae arborescens* var. *grandiflora* and was described as a new species. The aecia are deep

orange in color and more elongated than those of *P. Peckii*. The aecia appear on the under surface of the leaf in two parallel rows as shown in Figure 9C.

O and *I*. Follicolous.

Tsuga canadensis (L.) Carr., Bear Run, Lamar Gap, Clinton Co., June 24, 1919, J. F. Adams.



Fig. 8. *Caeoma abietis canadensis* on the terminal shoots of hemlock. The new terminal growth is dwarfed and curved like a "ram's horn".

12. *PERIDERMIIUM COLUMNARE* (Alb. and Schw.) Kze. and Schm.,
Deutschl Schwamme 10: 1815.

(*Calyptospora columnaris* (Alb. and Schw.) Kuhn).

A *Peridermium* on *Abies balsamea* was collected by C. R. Orton at Bear Meadows on July 8, 1916. In this vicinity the *Calyptospora* on *Vaccinium corymbosum* is very common. Field observations would indicate this *Peridermium* as the alternate stage. The infection is annual on the leaves of *Abies* spp., but perennial on the stems of *Vaccinium*. A witches-broom infection on *Vaccinium corymbosum* is shown in Figure 9A.

O and *I*. Follicolous.

Abies balsamea (L.) Mill., Bear Meadows, Centre Co., July 8, 1916,
C. R. Orton.

13. *CACOMA ABIETIS-CANADENSIS* Farl. Proc. Amer. Acad. Arts and
Sci. 20, 1885.

(*Melampsora Abietis-canadensis* (Farl.) Ludwig).

On the hemlock the new leaves, stems and cones are attacked by this rust. The aecial stage lacks a peridium, so is called a *Cacoma*. The new terminal growth is often dwarfed and in many instances much distorted and curved like a "ram's horn", Figure 8.

The leaves are much aborted and the new growth is killed by the season's end. On the cones it is most conspicuous in the sporulating stage with the mass of orange colored spores. Figure 7. Infected cones may be recognized in June. Usually every scale is infected and the mycelium ramifies throughout. The cones are killed by the rust and dry up and turn black but still adhere as a mummified growth. The writer and Orton established the relation of this rust by cultures on *Populus grandidentata* in June, 1915.

O and *I*. Caulicolous.

Tsuga canadensis (L.) Carr., Pine Grove Mills, Centre Co., June 13, 1915, C. R. Orton and J. F. Adams; Houserville, Centre Co., June 22, 1915, F. D. Kern and J. F. Adams; State College, Centre Co., July 4, 1916, C. R. Orton and J. F. Adams.

The following species of rusts which are known to have their alternate stage on some species of coniferous hosts have been collected in Pennsylvania. While field observations have not identified the alternate host, it is reasonable to expect they are established. In some instances, however, it is known that the uredinial stage on these hosts may perpetuate itself without the aecial host being present.

14. *COLEOSPORIUM TEREBINTHINACEAE* (Schw.) Arthur, N. A.
Flora 7:93, 1907.

(*Peridermium terebinthinaceae* (Schw.) Hedgecock and Hunt).

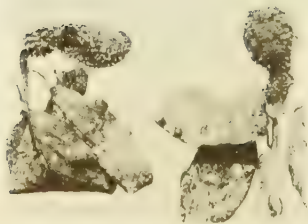
The uredinia and telia were collected by Orton on *Silphium tritoliatum*. Hedgecock and Hunt (*) established the relation of the *Peridermium* and *Coleosporium* by cultures in 1916. The aecia are reported on the leaves

*Hedgecock, G. G., and Hunt, N. R., A *Peridermium* belonging to *Coleosporium Terebinthaceae*. Phytopathology 7:67, 1917.

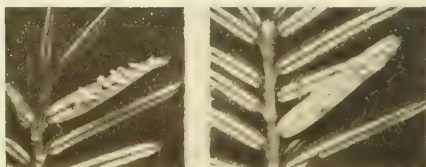
of *Pinus echinata*, *P. taeda*, and *P. rigida*. The II and III are known to occur on species of *Parthenium*, *Polymnia* and *Silphium*.



A



B



C

Fig. 9. (A) *Calyptospora columnaris* on *Vaccinium corymbosum* illustrating a small type of "witches-broom".

(B) *Gymnosporangium germinale* on the young fruits of Quince showing the cylindrical type of aecia.

(C) *Peridermium Hydrangeae* on *Tsuga canadensis* showing infection on two needles with the parallel rows of cylindrical aecia on the under surface.

II and III. On *Silphium trifoliatum* L., State College, Centre Co., August 18, 1916, C. R. Orton.

15. *MELAMPSORA BIGELOWII* Thuem. Mitth. Forstl. Vers. Oest. 2:37, 1879.

(*Caeoma Bigelowii* (Thum.) Arthur).

The uredinia and telia are commonly found on various species of *Salix*. The alternate stage is a *Caeoma* on *Larix* spp. It is known that this rust overwinters in the uredinial stage. At Charter Oak where our collections have been made there are no species of *Larix* known to be present.

II and III. On *Salix alba* L., Charter Oak, Huntingdon Co., August 8, 1913, F. D. Kern, C. R. Orton and J. B. Demarec; July 18, 1914, C. R. Orton.

Salix pentandra Muhl., Greenwood Furnace, Huntingdon Co., October 18, 1919, J. F. Adams.

16. *PUCINIASTRUM AGRIMONIAE* (Schw.) Tranz. Script. Bot. Hort. Univ. Petrop. 4:301, 1895.

The aecial stage of this rust has not been reported. The *II* and *III* are found on various species of *Agrimonia*. According to Arthur this rust has a distribution from Vermont to North Dakota, southward to Florida and Mexico; also in South America, Europe and Asia. In the vicinity where this rust has been collected a *Peridermium* resembling *P. Peckii* on the hemlocks is found. Next season it is intended to determine if this aecium has any relation to the rust on *Agrimonia*.

II and III. On *Agrimonia gryposepala* Wallr., Charter Oak, Huntingdon Co., August 17, 1914, C. R. Orton, A. A. Hansen and W. D. Canan; Galbraith's Gap, Centre Co., Sept. 14, 1916, C. R. Orton; Trout Run, Lycoming Co., Sept. 20, 1919, C. R. Orton and J. F. Adams.

Agrimonia parviflora Soland, L. D. Schweinitz (2835).

17. *UREDINOPSIS MIRABILIS* (Peck) Magn. Hedwigia 3:121, 1904.
(*Peridermium balsameum* Peck).

This rust has been collected only in the uredinial and telial stages at Bear Meadows and in Clinton County. It is known to infect several species of ferns. The aecia occur on the needles of *Abies* spp.

II and III. On *Onoclea sensibilis* L., Forestry Camp, Clinton Co., August 1, 1914, F. D. Kern and C. R. Orton.

Osmunda cinnamomea L., Bear Meadows, Centre County, August 24, 1919, C. R. Orton and L. O. Overholts.

18. *MELAMPSOROPSIS PYROLAE* (DC) Arthur, Result Sci. Congr. Bot. Vienne 338, 1906.

(*Peridermium conorum-piceae* (Reess) Arthur and Kern).

The *II* and *III* have been commonly observed in this vicinity on Shin-leaf. The aecia are known to occur on the cones of spruce. There are no spruces, however, in the vicinity where this rust has been collected. In some instances the rust appears to be perennial on the *Pyrola*, and observations would also suggest that it may overwinter in the uredinial stage.

II and *III*. On *Pyrola chlorantha* Sw. State College, Centre Co., May 5, 1891, W. A. Buckhout.

Pyrola elliptica Nutt., State College, Centre Co., May, 1897, W. A. Buckhout; April 14 and 28, 1913, C. R. Orton and J. F. Adams; May 5, 1914, J. B. Demaree.

19. *MELAMPSOROPSIS CASSANDRAE* (Peck and Clinton) Arthur, N. A. Flora 7:119.

(*Peridermium consimile* Arthur and Kern).

This rust has been collected by Orton and the writer on Leatherleaf in Bear Meadows. The *Peridermium* stage is known to occur on the needles of *Picea* spp., but has not been reported for Pennsylvania. This species has been reported to overwinter in the uredinial stage.

II and *III*. On *Chamaedaphne calyculata* (L.) Moench., Bear Meadows, Centre Co., July, 1914, C. R. Orton and J. F. Adams.

Eight species are reported for the second group of rusts belonging to the genus *Gymnosporangium*. Two of these species are important orchard diseases in the state on the apple and quince.

20. *GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE* Schw. Schr. Nat. Ges. Leipzig 1:74, 1822.

This is the well known apple-cedar rust and is very prevalent in the state, particularly in the southern counties. The telia are conspicuous in the spring, especially during a rainy period. They appear as orange-colored, gelatinous, horn-like outgrowths on globoid or reniform galls of the red cedar. The pycnia and aecia occur on the leaves and fruit of the apple as well as other species of *Malus*.

The aecial stage on apple has been reported from forty counties in the state. The most abundant distribution of this disease is in the

southern tier of counties. In Franklin and Adams Counties, which are the largest apple producing centers in the state, the most serious loss is reported from this disease. For the period 1908 to 1917, the annual loss from this disease in Pennsylvania was estimated to be .6%, equivalent to 128,943 bushels of fruit. In some instances the infection on apple leaves is so severe as to cause a premature defoliation. This loss may be prevented by careful destruction of all red cedars in the vicinity of the orchard. Infection on the cedar is generally prevalent throughout the state.

III. On *Juniperus virginiana* L., generally prevalent throughout the state. State College, Centre County, May 7, 1914, C. R. Orton and G. B. Demaree; Shingletown, Centre Co., April 25, 1916, J. B. Hill; very common in Pennsylvania, L. D. Schweinitz (3096).

21. GYMNOSPORANGIUM GLOBOSUM Farl. Anniv. Mem. Boston Soc. Nat. Hist. 18, 1880.

This rust develops a gall similar to the apple cedar gall and may be easily confused with the above species. The galls are irregularly globoid and the mycelium is perennial. The old telial scars may be observed, which differentiates it from the previous species. The alternate stage occurs on the leaves of apple and hawthorns. The aecia are cylindrical outgrowths on the under surface of the leaves. This stage has been observed commonly on various species of hawthorns. Schweinitz made one collection (2900) on *Pyrus communis* at Bethlehem, Penna.

III. On *Juniperus virginiana* L., generally distributed throughout the state. State College, Centre Co., 1891, W. A. Buckhout; Shingletown Gap, Centre Co., F. D. Kern, C. R. Orton and J. F. Adams.

22. GYMNOSPORANGIUM GERMINALE (Schw.) Kern, Bull. Torrey Club 33:506, 1908.

This rust has been observed to be quite destructive to the young growth of red cedars. The gelatinous telia develop on slight fusiform swellings and the mycelium is perennial. Figure 10. In the spring the reddish orange masses of telia are very conspicuous. The alternate stage occurs on the fruit of hawthorns, juneberry and quince. Terminal buds are often distorted and killed, as well as young stems. The aecia on the fruits are conspicuous cylindrical outgrowths, Figure 9B. In some sections of the state considerable loss has been experienced by quince

growers. In all instances the infection has been associated with the presence of numerous cedars. The destruction of the red cedars has eliminated the rust in one quince orchard.



FIG. 10. *Gymnosporangium germinale* on red cedar. The upper specimen shows the fusiform swelling of the stem before the telia have swollen. The lower specimen shows the gelatinous swelling of the mature telia after they have become moistened.

III. On *Juniperus virginiana* L., generally distributed throughout the state; State College, Centre Co., 1892, W. A. Buckhout; June 5, 1915, C. R. Orton; Delaware Water Gap, Monroe Co., May 30, 1917, F. D. Kern; Bethlehem, Lehigh Co., L. D. Schweinitz (3094).

23. GYMNOSPORANGIUM EFFUSUM Kern, Bull. N. Y. Bot. Gard. 7:459, 1911.

One collection of this rust has been made by F. D. Kern. The telia appear on long, slender fusiform enlargements on the branches of red cedars. The alternate stage is known to occur on *Aronia* spp.

III. On *Juniperus virginiana* L., Delaware Water Gap, Monroe Co., May 30, 1917, F. D. Kern.

24. GYMNOSPORANGIUM NIDUS-AVIS THAXTER, Bull. Conn. Exp. Sta. 107:6, 1891.

F. D. Kern and the writer collected this species on the red cedar in Monroe County, 1917. The mycelium is perennial in the branches, which often appear distorted. The alternate stage is known to occur on juneberry and quince.

III. On *Juniperus virginiana* L., Delaware Water Gap, Monroe Co., May 30, 1917, F. D. Kern and J. F. Adams.

The following three species are those known to be collected by Schweinitz in Pennsylvania:

25. GYMNOSPORANGIUM CLAVARIAEFORME (Jacq.) DC. Fl. Fr. 2:217, 1895.

The telia appear on long fusiform swellings of various sized branches on various species of cedar. The aecia are known to occur on hawthorns, quince, pear, and juneberry.

III. On *Juniperus communis* L., Pennsylvania, L. D. Schweinitz (3095).

26. GYMNOSPORANGIUM BOTRYAPITES (Schw.) Kern, Bull. Torrey Club 35:506, 1908.

The alternate stage on juneberry only has been reported by Schweinitz (2902). The telia occur on the white cedar, *Chamaecyparis thyoides*. Conspicuous fusiform swellings are produced on the branches of the cedar and the mycelium is perennial.

27. *GYMNOFORANGIUM TRACHYSORUM* Kern, *Mycologia* 2:237, 1910.

This species was collected by Schweinitz near Philadelphia in hedges of *Crataegus oxyacantha* L., (2899). The telia are reported by Kern as appearing on abruptly fusiform or somewhat gall-like enlargements on *Juniperus virginiana*.

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II. SEXUAL FUSIONS AND DEVELOPMENT OF THE SEXUAL ORGANS IN THE PERIDERMIIUMS*

J. F. ADAMS

Since the discovery of fertilization in the rusts by Blackman and Christman, considerable advances have been made in our knowledge of the sexual processes and the morphology of the aecidium. These studies, however, have been confined principally to forms parasitic on the angiosperms. I have undertaken to compare the development of the spermogonia and aecidia in several species representative of the form genus *Peridermium* with that of the forms previously studied.

There are still several points regarding the development of the aecidium about which further information is desirable. How do so-called confluent aecidia arise as compared with the ordinary simple cup? Does the peridium consist of metamorphosed aecidiospore initial cells or aecidiospores? Is the pseudoparenchyma composing the primordium of the aecidium made up entirely of the peripheral portions (sterile cells) of the gametophoric hyphae? Is the peridium in the stem forms more than one cell in thickness? Are these apical or sterile cells of the primordium to be considered homologous to the so-called "buffer" cells of the caeoma?

The genus *Peridermium* includes species possessing spermogonia and aecidia occurring on the trunk, branches or leaves of various gymnosperms. They are heteroecious, with their uredo sori and teleuto sori restricted to pteridophytes and angiosperms. They belong to the families, *Colcosporiaceae* and *Uredinaceae*, as found in Arthur's (2) classification of the North American *Uredinales*, and the *Melampsoraceae* according to Dietel (12).

The spermogonia of the leaf forms, *P. acicolum*, *P. balsameum*, *P. Peckii*, which I have studied, have long been known and described by the authors who have worked on these species. In the stem forms, *P. Comptoniae* and *P. pyritiforme*, the spermogonia have but recently been discovered.

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Weir and Hubert (43) first observed the spermogonia of *Peridermium Comptoniae* on *Pinus Banksiana*. "Several specimens of *Cronartium Comptoniae* bearing pycnial drops were secured by laboratory forcing methods following collection in the field". They describe the spermogonia in part as follows: "Pycnial stroma in irregularly shaped areas, more or less scattered or anastomosing, caulicolous, sub-epidermal, forming minute blister-like swellings when mature on unruptured infected tissues; exuding a clear, sweet, sticky fluid in which pycnosporos are suspended, forming drops of a cadmium yellow color when first appearing, becoming clear as the spore mass settles to the lower end of the drops and Brazil-red upon drying".

Boyce (8) first observed the spermogonia of *Peridermium pyritorme* on *Pinus ponderosa* near Castella, Shasta County, Cal., July 21, 1916. His description of the spermogonia is based on field notes and the examination of collected material. "Pycnia caulicolous, scattered, sub-epidermal, forming small, bladder-like swellings, exuding a clear, sweet, sticky Brazil-red liquid; Pycnosporos hyaline, commonly pyriform". He further states that "the pines are probably infected in the summer or fall of one season; pycnia do not appear until the summer of the next season at the earliest, while mature aecia are produced in the late spring or early summer of the third season".

Hedgcock, Bethel and Hunt (25) state that "the pycnia of *Peridermium pyritorme* Peck are borne on areas of the bark of pines contiguous to the aecia and preceding them one year. They are produced in the portions most recently invaded, commonly on the trunks and limbs. In case of both *Peridermium pyritorme* and *P. filamentosum* the pycnia most frequently appear at a date later in the season than the aecia".

Similar evidence of the alternation of the spermogonia and aecidia has been observed on *Peridermium cerebrum* by Hedgcock and Long (23). "From a series of field observations made by the senior writer during the last four years, it is established that in case of the swellings of *Peridermium cerebrum* on *Pinus virginiana* the pycnia precede the aecia 12 months instead of preceding them during the same spring. In other words, the pycnia and aecia occur during alternate years, and two years is the time required for a life cycle of all forms of spores of the rust".

Dodge and Adams (16) studied material of *Peridermium cerebrum* on *Pinus rigida* and *Pinus virginiana* collected in the vicinity of Lakehurst

and Tom's River, N. J., and Bedford, Va. The origin and character of the spermogonia were studied by removing the overlying bark and sectioning portions of the galls. In no instance did they discover spermogonia and aecidia on identical areas of the same gall. Certain galls were found developing only aecidia, others only spermogonia. In the Virginia material it was found in several instances that both developed on different parts of the same gall. Their observations indicate there is an alternation of the aecidia and spermogonia. The writers called attention to the crust-like spreading form of the spermogonium of *P. cerebrum* which disagrees strikingly with our ordinary conception of a spermogonium and so far seems to be characteristic of certain stem forms of *Peridermium*.

Shirai (39) has shown by culture experiments the connection of *Peridermium giganteum* (Mavr) Tubeuf and *Cronartium quercuum* (Cooke) Miyabe, which has been considered the same as the form of *Peridermium cerebrum* in North America (Arthur 2). He states that "the spermogonia of this fungus are formed in the month of January in the intercellular spaces between the corky bark and the cortical parenchyma as a flat continuous layer, when large yellow drops of viscous fluid of sweet taste loaded with an immense number of spermatia flow out from the fissures of the cracked bark. In consequence of the formation of the spermogonia and of the subsequent cracking of the corky bark, the pressure of the latter on the inner bark greatly lessens and thus secures the formation of the aecidial layers in the deeper tissues".

Spaulding (40) concludes from his observations of *Peridermium Strobi* on *Pinus strobus* (trees averaging from three to ten years old) that the spermogonia may develop at any time from early spring to late autumn. "Later, after a period of time of uncertain length (known in one instance to be about a year, the peridermium or aecidial spores are formed in pustules scattered over the swollen part".

The occurrence and distribution of the pseudoparenchyma was noted by some of the early students of the development of the parts of the aecidium primordium. Barclay (4) in *Aecidium Urticae* var. *Himalayense* mentions that the "basidia" rest upon a base of convoluted fibres forming a pseudoparenchymatous mass. De Bary (5) referred to the tissue above the hymenium in the young primordia as a pseudoparenchyma, which Richards (36) also mentions in connection with *Peridermium elatinum*. Sappin-Trouffy (38) in *Puccinia Liliacearum* finds that the

teleuto-sori are surrounded by a sort of pseudoparenchyma which envelops the young spores, while in *Peridermium Pini* a system of sterile cells entirely surrounds the base of the matured aecidium. Blackman and Fraser, (7) Hoffman, (26) and Fromme (20) have also described the distribution of the pseudoparenchyma in the various stages of the development of the aecidium.

Fromme (20) first described in detail the character and origin of the pseudoparenchyma above the fertile layer in the aecidium cup. "The first pseudoparenchyma cells formed are the apical cells of the hyphae that converge at the center of the hyphal mass. The disintegration of the cells of these hyphae proceeds from their apices towards their bases, and the area of pseudoparenchyma is increased by the addition of further cells on its margins. The apical surface of the mass is soon reached, and the sterilization of the hyphae then continues towards the lateral and basal surfaces". He further concludes that "the so-called 'buffer' cells of the caeoma are homologous with the pseudoparenchyma cells of the cup and represent a scanty production of pseudoparenchyma. The production of a peridium seems to be dependent on the presence of a considerable pseudoparenchyma, and this is in turn the result of the deep location of the primordium in the host tissue and the deep location of the gametes in the primordium".

Grove (22) in describing *Puccinia Caricis* speaks of the tissue of hyphal cells immediately below the fusion cells as a fusion tissue.

Blackman (6) regards the sterile cell that is cut off above the female cell in *Phragmidium violacearum* as an abortive trichogyne. The presence of sterile cells was found by Christman in the primary uredo sori of *Phragmidium potentillae canadensis* above the fertile layer. Olive (31) later regarded "such sterile cells as having but little phylogenetic significance, and as serving merely as 'buffer cells', to assist in rupturing the epidermis". In the caeoma types he investigated a sterile cell was generally present at the tip of only one of the gametes. Kurssanow (27) has referred to the sterile cells above each of the fusion cells in *Gymnoconia Peckiana* also as "buffer cells". Fromme (19) found two sterile cells above each of the gametes in *Melampsora Lini*. Blackman and Fraser (7) express some doubt as to the presence of definite sterile cells in the aecidium cup of *Uromyces Poae* and *Puccinia Poarum*. Dittschlag (13) observes an irregular development of the sterile cells in *Puccinia Falcariae*. The absence of definite sterile cells in the aecidium cup has been reported by

Pavolini (34) in *Uromyces Dactylidis*, Hoffman (26) in *Endophyllum Sempervivi* and Moreau (30) in *Endophyllum Euphorbiae* var. *uninucleatum*.

Moreau (30) does not agree with Fromme that the entire pseudoparenchyma is made up of sterile cells in *Puccinia violae*. She has designated the sterile cells as "preecidiospores" and holds that with the spermatia they represent respectively the female and male gametes which have lost their function. On the basis of the number of "preecidiospores" formed she considers the caeomas less specialized than the aecidium cup. While the preecidiospores are often developed irregularly in certain aecidium cups they may be entirely lacking in the higher forms such as *Endophyllum*.

Dodge (14), (15) has recently published an account of the development of the teleuto sori of six species of *Gymnosporangium*. He has found that the basal cell which gives rise to the teleutospores, always cuts off before spore development a cell which disintegrates. This is the ultimate or terminal cell which he considers here possesses a space-making or buffer function, although its original function may have been different. It is of further interest in that the first teleutospore bud generally pushes up through this terminal cell. This interesting discovery further establishes the fact that there is present a morphological unit in the teleuto sorus apparently homologous to the sterile cell, which previously had been thought to be confined to the aecidium.

Blackman (6) was the first to describe a real fertilization as the origin of the binucleate condition in the rusts. In *Phragmidium violaceum* he found the binucleate condition originating in a fertile cell as a result of a simple migration through a minute pore of a nucleus from a neighboring cell. This species was later reinvestigated by Welsford (44) who confirmed Blackman's earlier observation. So far, such a nuclear migration has been reported in but two additional species, *Uromyces Poae* and *Puccinia Poarum* by Blackman and Fraser (7). Christman (9) studied the origin of the binucleated condition in *Phragmidium speciosum*, *Cacoma nitens* and *Uromyces Caladii*. He found that the binucleate condition originates by the fusion of equal cells and later suggested that the nuclear migrations of Blackman might be pathological. Olive (31) observed early stages of cell fusion in *Gymnoconia interstitialis* and *Triphragmium Ulmariae*, which appeared similar to the nuclear migrations of Blackman. Pavolini (34) has described nuclear mi-

grations as well as cell fusions in the aecidium cup of *Uromyces Dactylidis* (U. Poae).

The method of fertilization by the fusion of equal cells appears to be the predominant type and has been reported in a large number of forms. In addition to those listed by Fromme (20) it has been described for *Phragmidium subcorticium*, *Puccinia Buxi*, *Uromyces Ficariae*, (30) *Peridermium cerebrum*, (16) and *Puccinia fusca*. (35).

De Bary (5) described the peridium as arising from the margin of the hymenium and developing therefore exactly in the same way as do the spore chains, but without forming intercalary cells. Sappin-Trouffy (38) and Grove (22) agree with De Bary that the peridium is composed of cells homologous with the spore mother cells. Fromme (20) finds that the first formed peridial cells are produced by a metamorphosis of apical aecidiospores which thus make up the central arch of the peridium, while the side walls are formed as lateral chains made up of modified aecidiospore initial cells rather than aecidiospores. Dittschlag (16) found the same method of forming the peridium in *Puccinia Falcariae*.

Plowright (36) stated that the peridium is formed in the same manner as the spore series, only the cells are sterile and empty. Christman (11) is also of the opinion that the peridium is composed of rows of abortive spores. However, these writers fail to advance any evidence in favor of their views.

Richards (37) was the first to observe the presence of intercalary cells in the peripheral chains of the aecidium. He found them in the aecidium on *Sambucus*. "The peridial cells, which become smaller and thinner walled as they approach the base of the hymenium, are seen finally to merge into a foot cell which exactly resembles the other basidia. In the youngest peridial cells even the interstitial cells were observed". "Very soon, of course, owing to the enlarging of the peridial cells and to the thickening of their walls, the interstitial cells disappear sooner than they do between the spores". Hoffman (26) and Moreau (30) have since demonstrated the presence of intercalary cells in the peridial chains of *Endophyllum Sempervivi* and *Puccinia violae*.

Kurssanow (28) was the first to show definitely that intercalary cells are cut off in the development of the peripheral chains. He studied the following species: *Puccinia graminis*, *P. grossulariae*, *P. phragmites*, *P. longissima* *Aecidium punctatum*, *A. ranunculacearum*, *Uromyces Poae*, *Endophyllum sempervivi*, *Gymnosporangium tremelloides* and *Perider-*

mium Pini. He concludes that intercalary cells are formed in the peripheral chains as well as in the interior chains, so that all of these peridial cells are morphologically aecidiospores which have become metamorphosed. One interesting exception he found in the peridial initial cells of the central chains in *Peridermium Pini*. The initial cells cut off the intercalary cells above so that for these apical mother cells of the central chain the position of the intercalary cell is reversed.

MATERIALS AND METHODS

During the spring session of 1916 at Columbia University some cytological work was undertaken on *Peridermium cerebrum* collected in New Jersey. The results were such as to lead to the further study culminating in the present paper. On returning to The Pennsylvania State College in 1917, material was collected for the basis of this problem. Professor C. R. Orton and Dr. J. R. Weir also supplied material. The work was continued at Columbia University during the college year 1917-18 under the direction of Professor R. A. Harper and Dr. B. O. Dodge. Acknowledgment also is made to The Pennsylvania State College and Dr. F. D. Kern for their assistance and cooperation in arranging for publication.

My material was chiefly collected in the field during the springs of 1916 and 1917. The five species studied are all eu-heteroecious forms, two have their aecidia on the trunks and branches of the pine, and the remaining three on the leaves of hemlock, balsam fir and pine.

Material was collected and fixed in the field. Flemming, Merkel and Bouin's fixatives were experimented with, and Flemming's in either weak or strong solutions proved most favorable. With the stem forms, *P. Comptoniae* and *P. pyriforme*, the best results were secured by cutting thin slices of the cortex and immediately immersing them in the fixing solution. Care must be exercised in handling the blocks which are to be sliced as the fruiting layers are fragile and easily disorganized. It is well to remove the overlying bark. Slices one-half inch in length may be handled satisfactorily. With the leaf forms small segments bearing the fruiting stages were cut out and immediately immersed in the fixing solution. On account of the abundance of resinous material in the hosts which appears to have a strong affinity for the osmic acid, at least 75 parts of the fixing solution should be used to 1 part of material. The material was kept in the fixing solution for 48 hours. It was kept in the

paraffin bath from 4 to 7 days at 55 C to secure perfect penetration before imbedding. Serial sections were cut with the rotary microtome from 5 to 8 μ in thickness. Flemming's triple and the iron haematoxylin stains were used. The former proved most satisfactory and was superior to the latter in differentiating the mycelium.

PERIDERMIIUM COMPTONIAE (Arthur) Orton and Adams.

Peridermium Comptoniae was collected on *Pinus virginiana* at Stone Valley and Charter Oak, in Huntingdon County, Pa. The alternate stage, *Cronartium Comptoniae* Arthur, is found on species of *Comptonia* and *Myrica* (41), Spaulding.

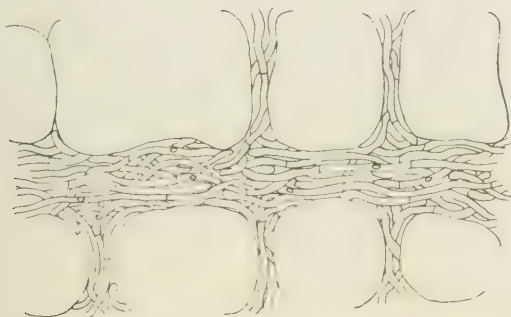
On *Pinus virginiana* this rust is found on the trunk where it develops irregular, semi-globoid swellings of various sizes and in the case of young trees the trunk is occasionally found girdled. In several instances the galls on the trunk were observed to extend below the ground. The swellings are usually rough in appearance with considerable dead bark adhering.

Material was fixed in the field on March 28, 1917, and March 23, 1918. At this time there was no external appearance of spermogonia or aecidia. Just below the bark a light yellowish zone could be observed which consists of the young primordia of the aecidia. Mature aecidia were not observed until May 12, 1917. At this time the aecidia on many of the galls were shedding spores.

The presence of mature spermogonia with abundant spermatia was observed in sections of material collected on the above dates. Exudations of spermatia such as are described by Weir and Hubert (43) were never observed in the field. On this host, owing to the dead bark that adheres to the galls, this exudation may be easily overlooked. However, the presence of spermogonia can be demonstrated if one carefully removes the overlying bark which is separable where the spermogonia develop. So exposed they appear as an extensive olive-green layer, irregular in outline.

Except for the haustoria, the mycelium is entirely intercellular and it branches irregularly. It is perennial in the host and is conspicuous in the green bark and phloem regions. In my material the mycelium can be traced into the wood for several annual rings where it appears to follow entirely the medullary rays. How old the galls were, I do not know. Haustoria are common in the cells of the phloem region and particularly in the cells of the medullary rays. They are constricted where the cell

wall is penetrated and a distinct unstainable zone is evident between the plasmamembrane of the host cell and the haustorium. They are of the same diameter as the mycelium and have a single nucleus. Several haustoria may be found penetrating a single cell. Usually one finds them in the vicinity of the nucleus of the host cell. In radial and tangential sections masses or fascicles of parallel hyphae may be observed as shown in Text Figure 1.

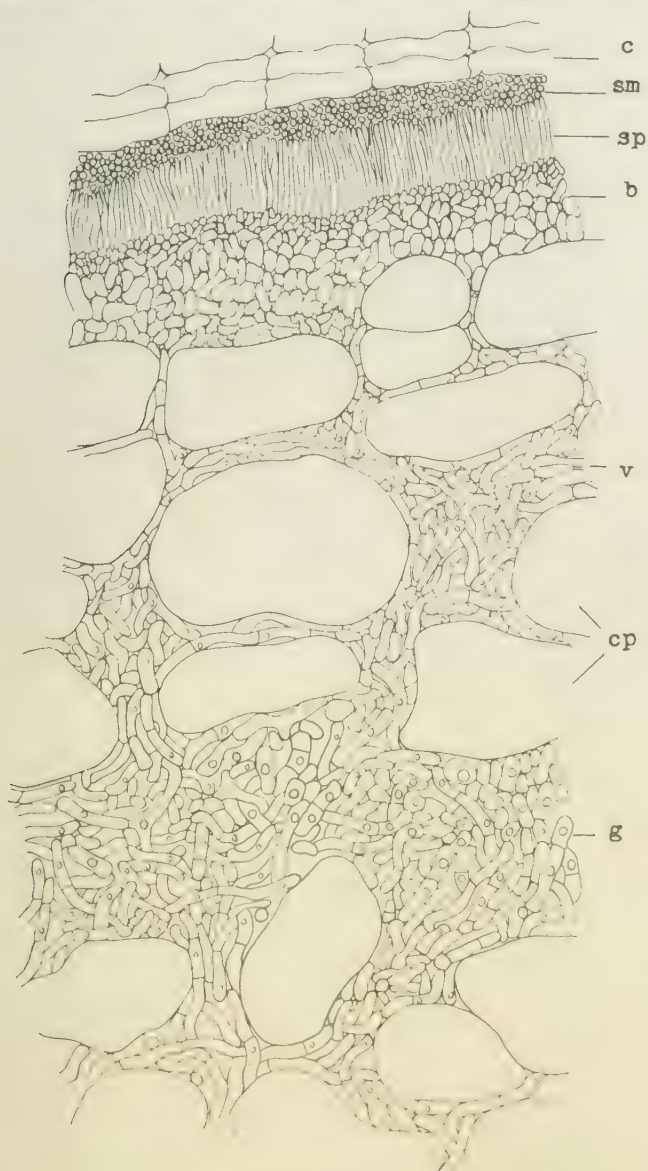


Text Fig. 1. *Peridermium pyriforme*. A mass or fascicle of parallel hyphae in the phloem region, from a radial section. X 480.

The cells making up the vegetative hyphae vary considerably in size and in breadth, averaging about 5 μ . In each cell a single globular nucleus is found. With the triple stain a small red nucleole is evident and the blue chromatin appears in small masses connected by delicate strands of linin.

The spermogonium appears as a broad, extensive layer of parallel spermatophores between the outer row of cortical parenchyma cells and the over-living thin walled cells of the phellogen. The latter cells become much disorganized. There is no definitely delimited margin of the spermogonial crust. It appears in this case as a young, spreading primordium or plectenchyma of hyphae as reported by Dodge and Adams (16) for *Peridermium cerebrum*. The spermatophores arise from a system of intertwined hyphae which make up a definite basal tissue. The cells in this basal tissue become enlarged and irregular in outline, staining very faintly. The spermatophores contain a single nucleus which is globular or elongated and the spermatia are abstricted from their free ends. No definite aperture in the host tissue was observed through which

Text Fig. 2. **Peridermium Comptoniae.** Section through the cortical region. C. Cork; Sm. Spermatia; Sp. spermatophores; B. basal tissue; V. vegetative hyphae; Cp. cortical parenchyma; G. primordium of the aecidium. This illustrates the appearance through a portion of a young aecidium primordium. The aecidia are first recognized by the massing of the hyphae between the host cells which are seen to be pushed apart. On the right side of this region the gametophoric hyphae are thicker and more closely septate with their direction of growth towards the surface of the host. The portion on the left is young and not differentiated, which is characteristic of the growing margin of the primordia. The hyphae in this region are not so compact and the intercellular spaces are larger. Only the thin walled cork cells are shown above the spermogonial layer and overlying there are found thick-walled suberized cells. X634.



TEXT FIGURE 2

the spermatia escape. The material collected in March and May showed abundant spermatia, often forming a solid, compact mass thicker than the spermogonium layer. Their escape is evidently dependent upon the irregular cracking of the overlying tissue.

The spermogonial layer was observed developing in the tissue overlying the aecidia as well as in the adjacent tissue. In some cases only three layers of cortical parenchyma cells separated the spermogonium and aecidium.

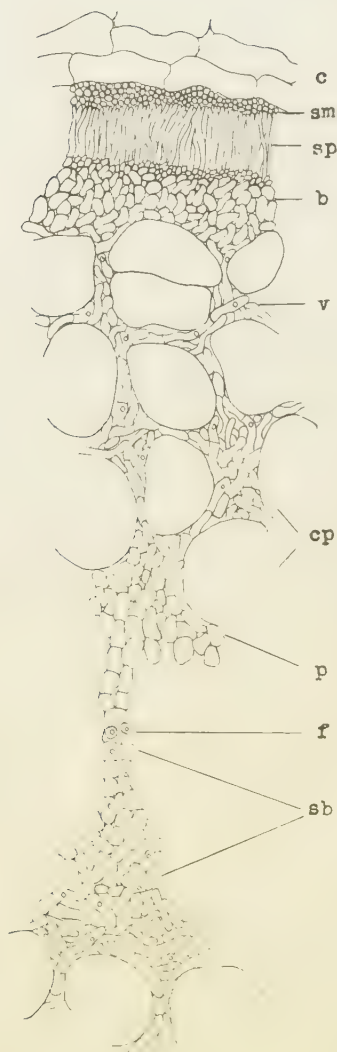
Two instances of internal spermogonia were found. In one case a definite conoidal type of spermogonium with spermatia, surrounded by several layers of vegetative hyphae, was found adjacent to the peridium of a mature aecidium. The normal spermogonial layer above was separated from this internal spermogonium by four layers of cortical parenchyma cells. It is of further interest that its direction of growth was towards the aecidium. The other case occurred with an excessive development of the basal tissue. On the surface a normal layer of spermatophores and below in the middle of the basal tissue another layer of spermatophores developed.

As previously mentioned, the primordia of the aecidia could be recognized in the field as early as March 23, when they appear in sections as a distinct yellowish zone. The primordia originate in the cortical parenchyma from 3 to 8 cells below the phellogen. Host cells adjacent to the primordia possess very thick walls and throughout the infected region many of the host cells are filled with a dark staining resinous or fatty substance. The cells of the hyphae making up the young primordia can be easily distinguished from the vegetative hyphae. They are rich in protoplasm with a conspicuous nucleus. They are shorter but thicker than the cells making up the vegetative hyphae. The primordia first appear as a massing of the hyphae between the host cells which are gradually forced apart as shown in Text Figure 2. This figure illustrates a portion of the developing primordium. The direction of growth of the hyphae is observed to be towards the surface of the host. On the left the primordium is young and not differentiated, while on the right the hyphae are more closely septate and thicker. In the young portion of the primordium the hyphae are not so compact. The intercellular spaces are conspicuous. With further development the primordium appears as a compact mass of hyphae as shown for *Peridermium pyritorme*, Plate 4.

As the primordium matures the hyphae appear in a definite palisade layer. These parallel hyphae may now be recognized as the gametophoric hyphae by their size and definitely oriented position. The uppermost cells of the gametophoric hyphae become enlarged and finally disorganization of their contents occurs. The cellular contents gradually recede from the wall as an irregular mass hardly differentiated with the stain. The nuclear membrane disappears and the nucleus later appears as an irregular, brilliant red object which eventually disappears. The uppermost cells of the gametophoric hyphae are the first to lose their contents, then the others below follow in sequence until a chain of five to eight such cells appears. These are the sterile cells which make up exclusively the pseudoparenchyma which overlies the fusion cells. Their position in relation to the gametes is identical with that of the sterile or buffer cells of the caecoma.

Below this layer of pseudoparenchyma the fertile cells are easily recognized. They are sharply differentiated with the triple stain by the density of their protoplasm and their large nuclei with a conspicuous nucleole in each. The nuclear membrane is distinct and the fine network with blue masses of chromatin is evident. The fertile cells are distinctly intercalary in position, as shown in Text Figure 3. In this figure it is shown that five or six sterile cells have been cut off above the fusion cells. Below at least three cells of their gametophoric hyphae may be recognized.

Fusion occurs between adjacent fertile cells of similar size and position in two gametophoric hyphae. A dissolution of the walls occurs usually at the upper ends where they come in contact. This phenomenon proceeds so as to result ultimately in the complete disappearance of the contact walls, thus forming a fusion cell. The term fusion cell is used to denote the immediate product of the fusion of two fertile cells or gametes and marks the transition from the gametophytic to the sporophytic condition. Plate 1, Figs. 4 and 5, represent two cells which have practically completed their fusion. When the lower parts of the walls have not completely disappeared it results in a two legged fusion cell. Such stages are very common. Immediately following fusion there occurs a considerable increase in the size of the fusion cells. This is indicated in Plate 1, Figs. 4 and 5, by the relative size of the two fusing gametes compared with their sub-basal cells. The nuclei become correspondingly larger and usually occupy the upper portion of the fusion cell where the cytoplasm is more dense.



Text Fig. 3. *Peridermium Comptoniae*. Section through part of the spermogonial layer and aecidium primordium. C. Cork; Sm. Spermatia; Sp. Spermatophores; B. basal tissue; V. vegetative hyphae; Cp. cortical parenchyma; P. pseudoparenchyma; f. fusion cell; Sb. sub-basal tissue. The spermogonial layer is seen to originate between the thin-walled cork cells and cortical parenchyma. The cells of the hyphae making up the basal tissue are poor in protoplasm. Host cells in the cortex are seen to be pushed apart by the vegetative mycelium. Only two gametophoric hyphae are shown. Above the fusion cell the continuity of the cells is still evident. These cells soon enlarge, losing their protoplasmic contents and are the sterile cells which make up the pseudoparenchyma. Fusion has been completed between two adjacent fertile cells of the gametophoric hyphae which are seen to be intercalary in position. Below the fusion cells is the sub-basal tissue which can be recognized by the size and shape of the cells compared with the vegetative mycelium below as well as their poorly stainable contents. X 489.

The sterile cells soon after fusion occurs enlarge, losing their contents, and become irregular in form. It is seldom difficult to follow their seriation with respect to their gametophoric hyphae

at the time of fusion. As many as eight sterile cells of a gametophoric hypha may be found. In Plate 1, Fig. 5, it was not positively determined that the sterile cells c and d were from the same gametophoric hypha as the gamete below. The irregular enlargement of the gametes and sterile cells after fusion is often confusing as to seriation. The apical cells of the gametophoric hyphae are the first to enlarge and lose their contents. They are the first pseudoparenchyma or sterile cells. The ones below follow in sequence till the gamete is reached. Thus the entire gametophoric hypha consisting of a series of cells not very different from each other becomes differentiated so that the uppermost cells disorganize to form the pseudoparenchyma, one functions as a gamete and the ones below the gamete make up the sub-basal tissue. Below the fusion cells the cells of the hyphae enlarge and the tissue is more compact at this time. This tissue below the fusion cells I refer to as the sub-basal tissue. The cells making up this sub-basal tissue do not take the stain as deeply and are sharply differentiated from the fusion cells above.

The primordium at the time of fusion appears as a broad mass of hyphae which have forced the host cells apart, thus causing disorganization of the host tissue. It varies somewhat in depth, possibly on account of the difference in resistance of the host cells at various points. Fusions progress uniformly with the centrifugal development of the primordium. The primordia are not blocked out or delimited as we find in the aecidium cups so far reported. What determines eventually the maximum development is not clear. The early unlimited development of the primordia is similar to what we find in the caecoma types. The more central areas of the aecidium may be matured as far as spore production is concerned without any indication that the margin has reached its limit of growth. The fusion of fertile cells was found in the developing primordia of the young regions in material collected as late as May.

After fusion is completed the cells enlarge as noted and cut off a spore mother cell. This occurs first in the more central regions of the matured primordia and progresses towards the young margin. Certain groups of fusion cells appear to be more precocious in their development. Some groups of basal cells produce a greater number of spore mother cells than those adjacent. Such a condition is shown in Plate 3. The outline of the peridial cells suggests this peculiar method of development. The term basal cell is used to refer to the fusion cell as it starts to cut off spores. It functions like a conidiophore and is thus similar to the basal cells in the uredo and teleuto sori.

After the spore mother cell is cut off it enlarges and then cuts off an intercalary cell below. These first spores of the central chains become metamorphosed to form the peridial cells of the central arch which in the stem forms is very extensive. The first formed spores do not retain their dense protoplasm as do those formed later. The nuclei soon become disorganized and break down and soon no stainable contents are observed in these cells. The cell walls of these initial peridial cells begin to increase in thickness and show a strong affinity for the Orange G. The peridial cells so formed vary much both in shape and size. At maturity their thickened walls, as has been frequently noted, become uniformly striated. Not only the first formed aecidiospore but the second, third, and even the fourth in the central chains become metamorphosed into peridial cells, as is shown in Plate 3. They have all cut off intercalary cells in the usual way, so that the central arch is found to be made up of a layer of metamorphosed spores at least two to four cells in thickness.

When the primordia have reached a certain degree of maturity, they become delimited by the formation of the peripheral chains of peridial cells. These peripheral chains are composed entirely of metamorphosed aecidiospores. The intercalary cells in these chains are not so conspicuous as are those in the central chains. They appear as if cut off from the lower outer edge of the peridial initial cell, as shown in Plate 2, Fig. 16.

In Plate 3 the pseudoparenchyma may be seen to be pushed upward with the maturing of the aecidium, but later it becomes disorganized and disappears. The overlying host tissue gradually ruptures irregularly and the so-called confluent aecidia become exposed.

PERIDERMIIUM PYRIFORME Peck

This rust was collected on *Pinus pungens* at Charter Oak, Pa. The alternate stage, *Cronartium pyriforme* (Peck), Hedgecock and Long, is found on various species of Comandra. I had for comparison material on *Pinus ponderosa* collected at Missoula, Montana, by Dr. J. R. Weir.

As reported by Hedgecock and Long (24) this rust on various species of two and three-leaved pines is characterized by the production of a slight hypertrophy resulting in either a fusiform enlargement or a globoid gall. On *Pinus pungens* practically no hypertrophy of the trunk is evident. Considerable dead bark is always found adhering to the galls, which makes it difficult to recognize an infected tree except when the fungus is sporulating. Material on *Pinus ponderosa* was characterized

by the production of fusiform enlargements. The infection on *Pinus pungens* was found upon the trunks of young trees close to the ground and occasionally upon some of the lower branches. (Orton and Adams 33). Infected trees were recognized May 20, 1917, when the aecidia were shedding spores. Young material was procured from around the young margin of infected areas.

The mycelium is perennial in the host, where it is found abundantly developed in the intercellular spaces of the cortex. The haustoria and mycelium have relations to the host cells similar to those described for *P. Comptoniae*. The host cells in the cortex are extremely large and appear to be hypertrophied.

The spermogonial crust on *Pinus pungens* appears pushing up between the outer layer of cortical parenchyma cells and the overlying thin walled cells of the phellogen. It is similar in appearance to the spermogonium of *P. Comptoniae*, consisting of a broad, crust-like layer of parallel spermatophores arising from a definite system of basal tissue. On the species of pines above mentioned the spermogonia were found developing in the tissue overlying the aecidia and that adjacent to them. In some cases the spermogonia and aecidia were separated by a layer three host cells thick, while in others the layer was ten host cells in thickness.

It was common to find the spermatia in extensive masses thicker than the spermogonial crust even in tissues overlying mature aecidia. There was no aperture for their liberation and it is probable few of them escaped unless very late in the season, when more disorganization of the cork tissue had occurred. The spermatia are commonly pyriform, a character possessed also by the aecidiospores. A section through a portion of a young aecidium primordium is shown in Plate 4. On the left the advancing margin consists of intertwined cells rich in protoplasm and with prominent nuclei as compared with the vegetative hyphae. The growth of the hyphae at this point is in part directed towards the surface of the host as well as in the direction of the spreading primordium. In this the direction of growth of the gametophytic hyphae is not towards any central point as described for other forms of the aecidium cup. In the figure in Plate 4 the gametophytic hyphae on the right are seen to have their direction of growth entirely towards the surface. The cells making up these hyphae are shorter and thicker, forming a distinct palisade layer such as is found in *P. Comptoniae*. Further to the right of this section drawn, the aecidium showed progressively greater and greater maturity.

with fusion cells and basal cells that had cut off peridial cells as well as spores. The apical cells of the gametophoric hyphae shown in this figure have not started to disorganize. Their protoplasmic contents and nuclei are intact. They are the sterile cells which later make up the pseudoparenchyma overlying the fusion cells. I was unable in this case to trace these gametophytic hyphae directly to the sub-basal tissue of the spermatogonia. They may be observed extending beyond the primordium and between the overlying host cells.

The gametes or fertile cells may be recognized by their size and dense protoplasm. There is no definite number of sterile cells above the gametes. When the primordia are deep seated the number of sterile cells is greater, varying from 4 to 10.

Fusion occurs, as in *P. Comptoniae*, between fertile cells in two gametophytic hyphae of approximately the same size and similar position. They are very common and these stem forms have proved the most favorable for demonstrating cell fusion. Their size and definite position make them easily recognized. Early fusion is shown in Plate 1, Figs. 1 and 3, where the dissolution of the two walls has resulted in a small opening. The lowermost sterile cells a, b, c, and d in Fig. 3, are shown above their respective gametes. This dissolution of the walls usually proceeds to the base. After fusion is completed, the fusion cell enlarges in length and width with a corresponding increase in the size of the nuclei and nucleoli. Figs. 7 and 8 are two-legged basal cells. Fig. 6 shows a peculiar multiple fusion between four fertile cells which I consider an aberrant condition. It may result in a multi-nucleated basal cell such as have been found in accidium cups, as reported by other investigators.

The accidium is similar in development to that I have described for *P. Comptoniae*. They are not blocked out before maturity. Their limitation is fixed only by the appearance of the peripheral peridial chains.

Each of the first accidiospore mother cells formed cuts off an intercalary cell below and the accidiospore itself becomes metamorphosed to form the peridial cell of the central arch. In this form the peridium is throughout but one cell in thickness. The cells are more uniform in size than in *P. Comptoniae*. In some instances one appears to be above another, but since they are crowded close together it is possible some get pushed aside. In the field the peridium was always observed to be evanescent, which may be associated with the fact that it is but one cell in thickness. The central arch of the accidium is entirely made up of the

apical metamorphosed aecidiospores. The delimitation of the aecidium now is evident by the peripheral peridial chains. These peripheral chains are made up of metamorphosed aecidiospores as shown in Plate 2, Fig. 17.

The aecidiospores are characterized by their pyriform appearance. The spores on *Pinus raugens* are larger and more distinctly pyriform than those on *Pinus ponderosa*. The spores have been described by Arthur and Kern (3), and Hedgecock and Long (24), as being narrowed and acuminate below. I find the spores still attached in chains with their upper ends narrowed. A noticeable thickening of their cell walls occurs when the spores are about the third or fourth from the basal cell. The upper end of each spore then becomes acuminate and the wall at this end is much thicker than at the base. The cytoplasm may be observed extending as a thread-like mass into the thickened acuminate end.

PERIDERMIIUM ACICULUM *Underwood and Earle*

This rust was collected on the leaves of *Pinus rigida* at Pine Grove Mills, Pa. Material for study was obtained at different times throughout the spring of 1917 from a single tree. The infected needles were recognized as early as March 1, 1917, when there appeared on them pale, yellowish bands varying in length from 2 to 5 mm. Such infected areas were not restricted to any part of the needle and from one to three such areas could be found on a single needle. In this respect the external characters of the infection agree with those described for *Gallowaya Pini* by Galloway (21).

Material collected March 1, 1917, was found to possess matured spermogonia with spermatia on either side of the needles. The mycelium is not distributed throughout the leaf, but is found restricted to the areas of discoloration above mentioned. The hyphae are very large and conspicuous, averaging 6.5 μ in diameter. The cells contain a single, large nucleus. The hyphae may be recognized between the cells of the mesophyll and in places the palisade cells are often disorganized.

The spermogonia are conoidal in outline, as seen in vertical section, developing between the palisade and hypodermal cells and raising the epidermis. Surrounding the spermogonia are several rows of parallel cells similar in appearance to those from which the spermatophores arise. This fruiting structure is definitely blocked out and is not unlimited like that of the two preceding species. The spermatophores arise from a deep layer of basal tissue, the cells of which have practically no stainable contents

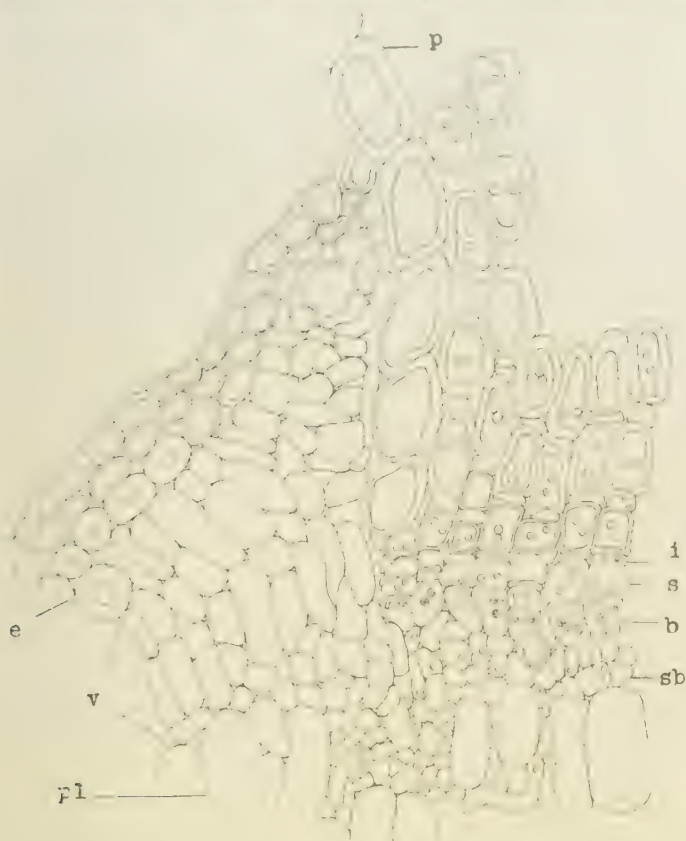
and where nuclei are evident they appear disorganized. The spermatophores are larger and longer than those in the stem forms and are seen to bend towards a central opening or aperture. The spermatia are large with prominent nuclei and little cytoplasm. They ooze up through the aperture and are found to adhere in masses on the leaf surface surrounding the opening.

Accidial primordia were first found in material collected May 25, 1917. Like the spermogonia they develop on both surfaces of the needle, opposite or adjacent to the spermogonia. The gametophoric hyphae are arranged in a definite palisade as shown in Plate 5. Their direction of growth is towards the leaf surface. The gametes or fertile cells are easily recognized by their deeply staining contents. Above the gametes is found a layer of sterile cells 4 to 8 cells in thickness. These sterile cells soon lose their protoplasmic contents and appear like those described for the stem forms. The pseudoparenchyma is made up entirely of sterile cells. This mass of hyphae is pushed upwards following the production of spores and gradually disappears about the time the accidia are rupturing the overlying tissue.

The gametes are much larger than those described in the previous forms. The shallow sub-basal tissue is found to be made up of only two or three cells below the gametes (Plate 5). Fusion stages agree in all respects with those already described. Plate 2, Fig. 13, shows a complete fusion. In the early primordia the fusions are very common, but two-legged basal cells are not frequently found. Fusion between the gametes proceeds from the center to the margin of the accidium. The first peridial initial cell, cut off from the basal cells, behaves differently than it does in any other forms I have studied. The intercalary cell instead of being cut off in the usual way is cut off at the upper end of the initial cell. This interesting deviation is easily recognized in the early stages of the accidium up to the time of rupturing the epidermis. The intercalary cells are large and persist for some time after the peridial cells are mature. Plate 1 and 2, Figs. 10, 14, and 15, illustrate three basal cells. Nos. 10 and 14 have cut off the first initial cell which has divided into the intercalary cell above the peridial cell below. Fig. 15 shows the terminal intercalary cell and peridial cell as well as the first accidiospore with intercalary cell.

The accidium in this form is early delimited by a surrounding layer of vegetative cells, several cell layers in thickness. These cells become elongated towards the surface of the leaf and may possibly assist in pushing

up the overlying host cells. They lose their protoplasmic content like the sterile cells, but do not become disorganized like the latter. Sappin-Trouffy (38) has referred to this layer in *Peridermium Pini* as a layer of sterile cells. He shows them extending up beyond the epidermis



Text Fig. IV. *Peridermium acicolum*. Cross section showing margin of matured acicolum. E, cuticle, epidermal and hypodermal cells; V, vegetative cells; P, palisade parenchyma; Sb, sub-basal tissue; B, basal cells; S, acidiospore; I, intercalary cell; P, Peripheral peridial chain. The peridium is thickened out by a layer of sterile cells. These lose their protoplasmic contents like the sterile cells and become elongated towards the leaf surface and may possibly assist in pushing up the overlying host cells. The sub-basal tissue is very shallow, being made up of only two or three cells. Near the base of the peripheral peridial chain three of the spores still show the intercalary cells which are cut off from the lower outer edge in contrast to the central spore chains. X 444.

with some of the terminal cells swollen as though they were paraphyses. In Text Fig. 4 the margin of a matured aecidium is shown. This layer of vegetative hyphae (v) is adjacent to the peripheral peridial chains.

The peripheral chains of the aecidium cup are made up of metamorphosed aecidiospores, as shown in Plate 2, Fig. 18. The inner walls of the peridial cells in these chains are thickened and uniformly striated.

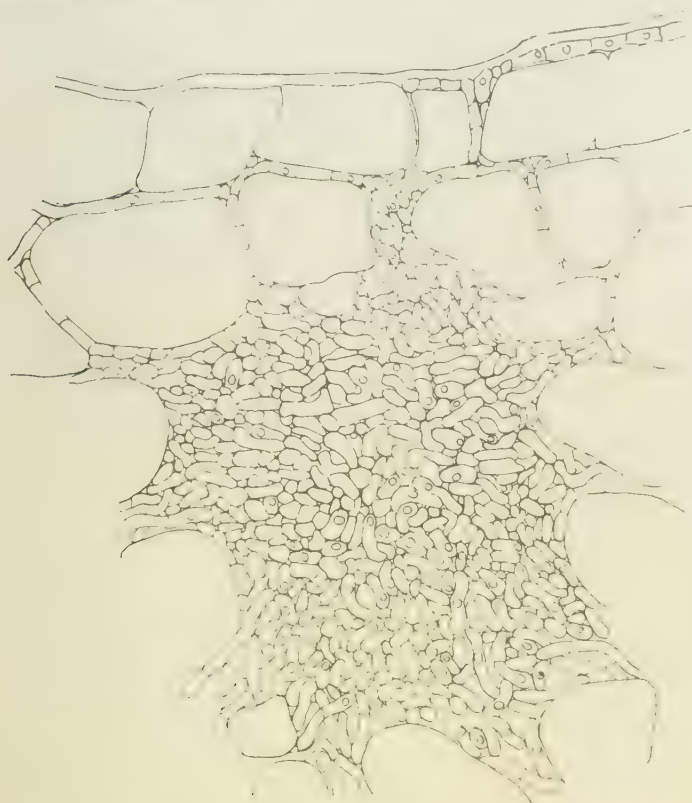
PERIDERMIIUM PECKII *Thuem.*

Material was obtained on the leaves of hemlock in the vicinity of Pine Grove Mills and Charter Oak, Pa., where several species of *Vaccinium* were found infected with *Pucciniastrum Myrtilli* (Schum.) Arthur, which would indicate that this is the alternate stage. On the leaves this rust forms two rows of conspicuous cylindrical aecidia which are erumpent on the under surface. The infected leaves are light yellow and may be easily recognized before the aecidia rupture the epidermis. Mature aecidia were found May 20, 1917. The mycelium is intercellular and distributed throughout the leaf. The hyphae are about $4\ \mu$ in diameter.

In this leaf form the spermogonia develop subcuticularly. They arise from a conspicuous layer of hyphae, pushing up between the epidermal cells, and forming a definite weft under the cuticle. Arthur and Kern (1) have described them as developing on the under surface of the needle. I have found them frequently on the upper surface, but more commonly on the under surface. From the weft of subcuticular hyphae the spermatophores arise in a parallel series with their free ends curving towards a small aperture in the cuticle. In outline the mass is conoidal to cylindrical. They vary much in size, ranging from 38 to $57\ \mu$ in height, by 114 to $228\ \mu$ in length. In many instances they appeared confluent. The subcuticular hyphae could often be traced in longitudinal sections, the entire length of the leaf, with spermogonia appearing at irregular intervals. Paraphyses were occasionally found in some of the spermogonia, but this does not appear to be a uniform character. There is a definite basal tissue as described for the previous species.

The aecidia have their origin in the spongy parenchyma where they appear first as a tangled mass of hyphae. In the early stages of the primordium the tangled hyphae are more regular in septation and richer in protoplasm than the cells of the vegetative mycelium. The primordium is similar to that found in *Peridermium balsameum*, Text Fig. 7. This young primordium increases in size, its greater growth being towards the surface. With this growth there is a corresponding increase in the

size of the hyphae, but it still appears as a compact interlaced mass, as shown in Text Fig. 5. The hyphae cannot be traced with certainty. When the upper cells of this mass begin to lose their protoplasmic contents and appear irregular in outline, the hyphae at the base appear more definitely oriented and their direction of growth is towards the center of



Text Fig. 5. *Peridermium Peckii*. Cross section through leaf primordium, peridermium primordium. At this stage the primordium appears as a compact interlaced mass of hyphae. The upper half of this mass towards the epidermis shows no definite direction of growth. This is the part that first becomes disorganized. At this stage the cells have enlarged somewhat and are easily recognized by their loss of protoplasmic content. Hyphae in these the hyphae can be seen to be somewhat more oriented and uniform. The cells making up this region are easily differentiated by their dense, solid, and for the most part, regular hyphae. X 562.

the primordium, Text Fig. 6. In this figure the cells in the upper part of the primordium assume the appearance of the sterile cells in the other forms. Whether these apparently sterile cells are the peripheral cells of the gametophoric hyphae could not be made out clearly. This upper mass of cells, however, appears as a definite pseudoparenchyma. The gametophoric hyphae at the base of the primordium make up a fertile region, the cells of which are conspicuously characterized by their dense protoplasm. The base of the primordium continues to widen up to the time of fusion. The definite palisade arrangement of the gametophytic hyphae noted in the previous forms is lacking.

Fusions appear in the central part of the fertile tissue and proceed towards the margin. In some instances two to four sterile cells were observed above the gametes. The early formed pseudoparenchyma is thus enlarged by sterile cells from the gametophoric hyphae. The fusion of gametes is similar to that described for the species on pine. Plate 1, Fig. 2, shows an early stage of fusion between two gametes. At the top where the two gametes first come together a dissolution of the walls has occurred, resulting in a small pore. This dissolution usually continues till the adjoining walls have been dissolved. It is seldom that two-legged basal cells are found in this species. The fusion cell elongates and the two nuclei take up a position in the upper half. The fusion cells are broad at the upper end with a narrow base.

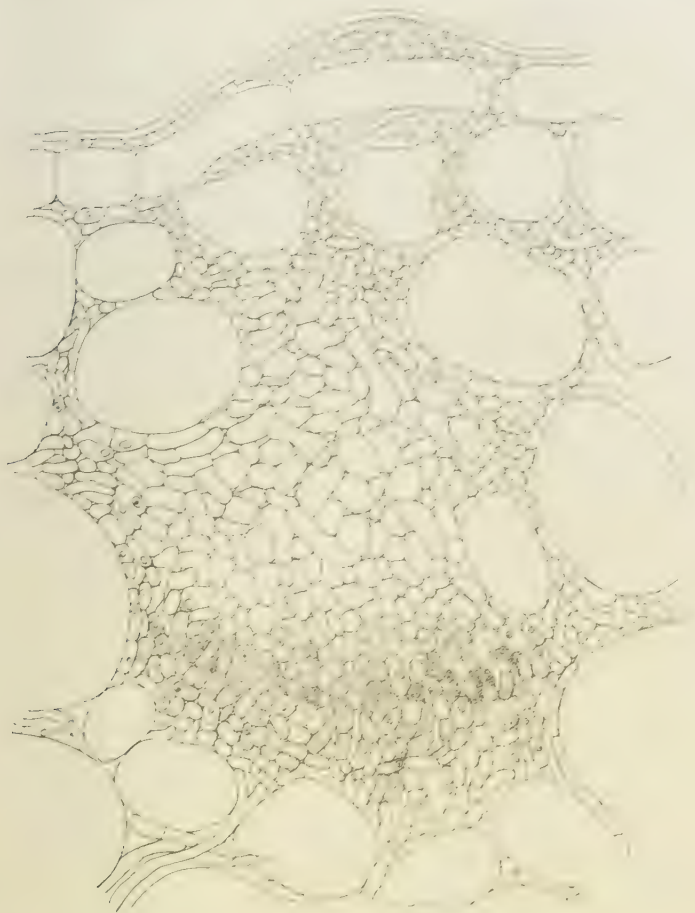
Below the fusion cell the hyphae enlarge and make up a definite sub-basal tissue. The contents of these cells take the stain lightly and the nuclei are not easily recognized. In this leaf form the accidium cup is soon definitely limited as a sharply blocked out primordium.

The peripheral part of the peridium is made up of metamorphosed accidiospores as shown in Plate 2, Fig. 19. The peridial cells are thickened on their inner walls and are elongated. A distinct overlapping of the end walls is found in these peridial chains.

PERIDERMUM BALSAMEUM Peck

Material was collected by Professor C. R. Orton, at Walden, Vt., on the leaves of *Abies balsamea*. Field observations point to species of *Onoclea* and *Osmunda* as being the alternate hosts, thus identifying it with *Uredinopsis mirabilis* Magn. as previously shown by Fraser (18).

The accidia are formed irregularly in two rows on the under side of the leaves. The infected leaves are yellowish in appearance and do not



Text Fig. 6. *Peridermium Peckii*. Longitudinal section through leaf showing later stage of primordium than in Fig. 5. The cells in the upper part of the primordium assume the appearance of sterile cells making up a definite pseudoparenchyma. Whether these apparent sterile cells are the terminal cells of the gametophoric hyphae could not be made out clearly. The protoplasmic contents are indicated in the cells making up the fertile region. The gametophoric hyphae in this region are more definitely oriented than in the preceding figure with their direction of growth towards the center of the primordium. The base of the acidium contains a small, dark, circular spot. The acidia are more delimited; matured acidia are cylindrical in form and more deeply seated in the leaf tissue than in the case of *P. aciculum*. X 560.

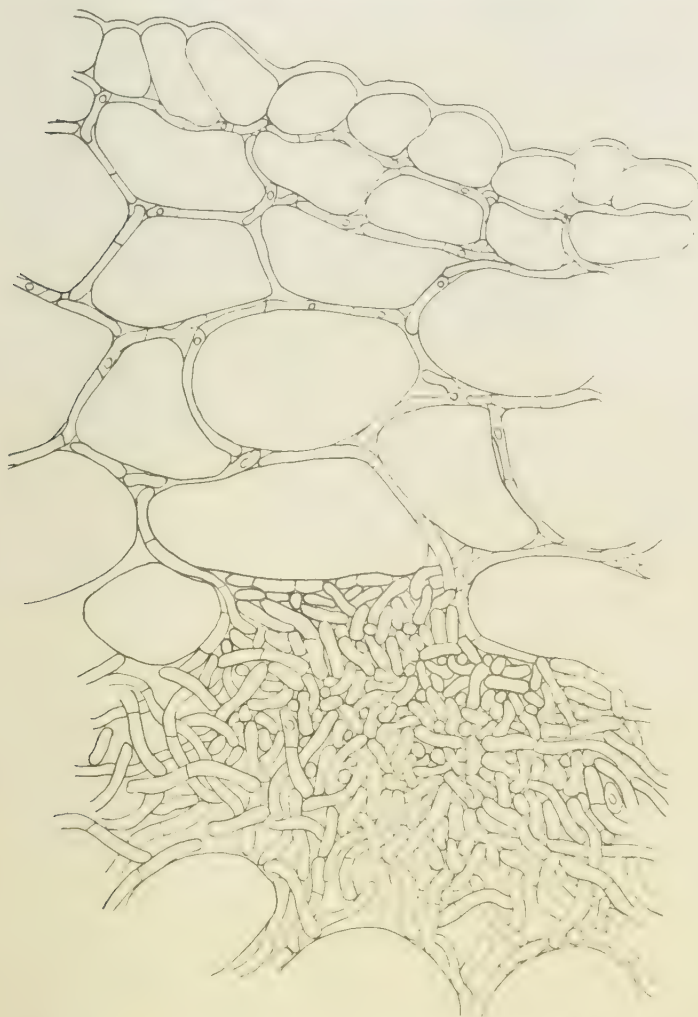
show any change in form. The mycelium ramifies throughout the tissues of the leaf, averaging $4\ \mu$ in thickness.

The spermogonia are commonly found developing on both surfaces of the leaf. Arthur and Kern (1) have described them only on the under surface. They are subcuticular in origin and extend into the the epidermal layer. In outline they are hemispherical, but are slightly raised above the leaf surface. They are irregularly distributed and I found no extensive sub-cuticular mycelium such as is present in *P. Peckii*. The spermatophores arise from a well-developed basal tissue. They are broad at the bases, short and tapering towards their free ends which converge towards the upper central region of the hemispherical fruit body. The spermatia are elliptical and pointed at both ends.

The aecidium primordium has its origin in the spongy parenchyma, usually 5 or 6 host cells in depth, as shown in Text Fig. 7. It is situated between the central fibro-vascular bundle and the lateral resin ducts. A young primordium is shown in Text Fig. 7 at the stage when it appears as a compact mass of intertwined hyphae which are rich in protoplasm. This primordium increases in size, the direction of growth being towards the lower epidermis, where it pushes apart and causes a disorganization of the overlying cells.

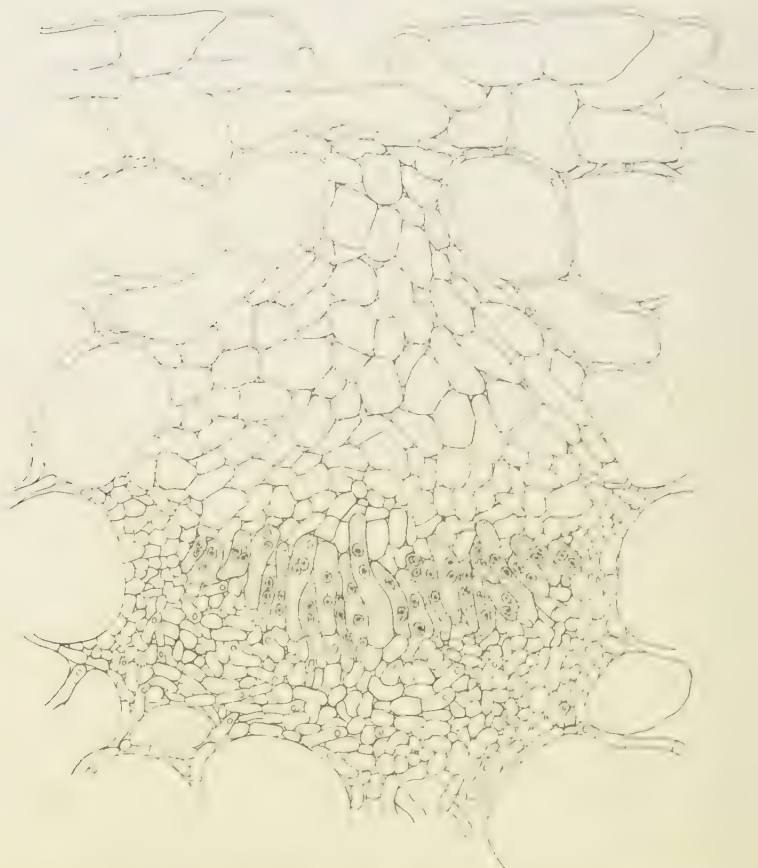
The upper portion of the primordium at the time of fusion is made up of cells which are irregular in outline and appear like the pseudoparenchyma in the preceding species. A fertile layer making up the base of the primordium is distinctly recognizable at this stage. The gametophoric hyphae are very irregular in this fertile region. They do not become so characteristically oriented as in the preceding species, as some are perpendicular and others horizontal to the leaf surface.

Fusions first occur between the gametes in the central part of the fertile region and proceed towards the margin. They may take place between gametes in the perpendicular as well as in the horizontal hyphae of the fertile region, but not at the same level. Two or three sterile cells may be cut off above some of the gametes. Two complete fusions are shown in Plate 2, Figs. 11 and 12, and Plate 1, Fig. 9. After fusion the cells elongate towards the pseudoparenchyma. The two nuclei usually occupy the upper end of the fusion cells as shown in Text Fig. 8. After the fusion of gametes is completed in the fertile region they appear usually to lie in about the same plane. Plate 1, Fig. 9, shows a basal cell in which conjugate nuclear division has occurred. The basal cell



Text Fig. 7. *Peridermium balsameum*. Cross section through host showing early appearance of aecidium primordium in the spongy parenchyma. It appears as a compact mass of interlaced hyphae which are rich in protoplasm. As the primordium increases in size, the direction of growth is towards the lower epidermis where it pushes apart and causes a disorganization of the overlying cells. X 650.

now divides, cutting off the aecidiospore initial cell containing two daughter nuclei. This cell enlarges and soon divides, forming the aecidiospore and a small intercalary cell. The first spores cut off become



Text Fig. 8. *Peridermium balsameum*. Longitudinal section of leaf with aecidium primordium just after fusion of gametes has been completed. The basal cells are shown with their nuclei and protoplasmic contents. Above these the meristematic cells making up the pseudoparenchyma are still intact. The resulting tumor cells elongate considerably before cutting off the first aecidiospore initial cell. X 595.

metamorphosed to form the peridial cells of the central arch, which extends from the center to the lateral basal cells. The production of spores then follows. The overlying pseudoparenchyma is pushed up-

wards with this development, becoming much disorganized and eventually disappearing. The epidermis, which is arched upwards, is soon reached by the developing aecidium. The peripheral chains are similar in origin to those already described, Plate 2, Fig. 20.

DISCUSSION

In the five species studied extreme variation is found in the type of the spermogonial fructification between the stem and leaf forms. The spermogonia for the stem forms of *Peridermium* have not hitherto been consistently described. Under the genus *Cronartium* they are described in part as being shallow and hemispherical by Grove (32), Fisher (17), Dietel (12), while Arthur (2) refers to them as deep seated, broad and flat. Sydow (42) refers to them as "sub-epidermalia, profunde immersa majuscula".

Shirai (39) has noted that the spermogonia develop in January and are a flat continuous layer in *Peridermium giganteum*. If this form is to be considered the same as *P. cerebrum* it differs from the latter in the relation between its spermogonia and aecidia. Shirai finds the aecidia develop in the tissue immediately below the spermogonia (Plate 4, Fig. 3), so that there is no alternation of spermogonia and aecidia as found in *P. cerebrum* by Hedgecock and Long (23) and Dodge and Adams (16). As noted the former writers state that the spermogonia precede the aecidia twelve months.

In describing the spermogonia of *P. Comptoniae*, Weir and Hubert (43) use the terms "spermogonial stroma". Just what is meant by the use of the word "stroma" is not very clear. The statement that the spermogonia are scattered or anastomosing, would imply that they consist of separate units and the stroma would be the result of these units fusing to form a single one. Boyce (8) has referred to the spermogonia in *P. pyriforme* as scattered, but no mention of their crust-like character is made. In both these species the spermogonia are referred to as blister or bladder-like swellings without specifying the extent of the single blisters. In this sense the description would hardly agree with my observations or Arthur's (2) description for the genus *Cronartium*. In the material of these two stem forms I have studied, no evidence of alternation of the spermogonia and aecidia was found.

Sections a half inch in length of a continuous spermogonial layer have been made in these stem forms. Their position may best be seen

nized if the overlying bark is carefully removed. They are irregular in outline and the margins are not delimited, but consist of a developing plectenchyma or anlage. The spermogonial layer appears as a broad flat crust-like layer. Owing to the time when material was collected, it could not be determined definitely when the spermogonia originate. There were no indications that the extensive crust-like areas were made up of separate units that had become confluent. In some instances small areas were observed separated from the more extensive crust-like area because of the irregularity and dipping of the cork layer.

The matured spermogonial layer consists of erect spermatophores which arise from a basal tissue and in height average from 35 to 40 μ . Its height is very irregular owing to the variations in the development of the basal tissue which fills in the uneven interstices between the cork layer and cortical parenchyma and possibly to the resistance of the overlying cork layer. The cells making up this basal tissue are poor in protoplasm. The spermatophores are much shorter and thicker than they are in *P. cerebrum*, averaging in length about 25 μ . Two spermatophores were commonly found to be developed from a single basal cell.

As previously mentioned there is no definite aperture for the escape of the spermatia, which apparently depend for their escape upon the irregular cracking of the overlying tissue. In this respect they are different from the leaf forms studied, which possess a definite aperture or ostiole. The extensive development of the spermogonial layer in these two stem forms is an interesting deviation from our ordinary conception of a spermogonium and further study may establish this type as being characteristic of the stem forms.

Arthur and Kern (3) describe the spermogonia as forming minute, bladdery and scattered swellings, in *Peridermium Strobi*, while Grove (22) describes them as irregular elevations of the bark, 2 to 3 mm. broad, although cytological evidence is wanting as to their exact nature and development.

Considering the apparently unlimited development of these spermogonia in the stem forms I have studied, we may characterize them as a caecomoid type of fructification. These caecomoid spermogonia originate between the cork layer and cortical parenchyma and thus are to be considered cortical, not sub-epidermal, in origin. The effect of the development of the spermogonia and aecidia is such as to kill the immediately adjacent tissue. This tissue is sloughed off in the late summer with the formation below of a new cork layer.

Fromme (20) has shown that the pseudoparenchyma above the fertile layer in the aecidium cup is made up of sterile cells and considers them homologous with the sterile cells or buffer cells in the caecoma. We find in the caecoma only a scanty production of pseudoparenchyma. That this tissue represents a specific morphological unit is evident, whether its cells formerly acted as trichogynes or were potentially gametes. So far we can only conjecture their earlier functions. In the caecoma and aecidium this tissue is certainly of similar origin in relation to the gametes. Its scant production in the caecoma may be correlated with the precocious fusions which occur in the gametic hyphae. Fromme (20) has suggested that the tendency to produce more than one sterile cell in the caecoma is seemingly a transition towards the condition found in the aecidium cup. On the basis of the scant production of the pseudoparenchyma in the caecoma, one might assume that it is primitive. Moreau (30) page 126, makes the statement that "the caecomas appear to be the least specialized of the aecidial fructifications as they exist, the preaecidiospores (sterile cells) are still sometimes all present; they are not formed except with irregularity in certain aecidia more specialized than the caecoma and are entirely lacking in the most specialized aecidia (Endophyllum)". But it is to be noted that in such forms also a mass of large, empty cells is found above the fertile layer. In position it corresponds to the pseudoparenchyma we have already discussed. Moreau (30) characterizes the greater portion of the tissue above the fertile cells in *Puccinia violae* as vegetative. I have been unable to determine definitely whether the pseudoparenchyma in *P. Peckii* and *P. balsameum* is made up entirely of sterile cells cut off from the gametophoric hyphae. Such cells are certainly not lacking, but the upper part consists of such an intricately interlaced mass that the gametophoric hyphae of the tissue cannot be traced with accuracy.

The evidence as to the origin of the pseudoparenchyma from sterile cells of the gametophoric hyphae in *P. Comptoniae*, *P. pyriforme* and *P. acicolum* is most convincing. The gametophoric hyphae form a conspicuous palisade layer in these forms. Further investigation of other species of *Peridermium* may prove this morphological character to be of some significance as contrasted with its absence in the aecidia so far investigated on the angiosperms. I have observed in these forms that sterile cells are always present above the gametes. The pseudoparenchyma is sharply defined from the fertile layer and my observations agree with those of Fromme that it is made up of sterile cells of the gameto-

phoric hyphae. The function of this tissue is evidently that of space-making.

The ultimate or terminal cells described by Dodge (14, 15) in the teleutosori of *Gymnosporangium* are, whether or not homologous with them, certainly similar to the sterile or buffer cells. They apparently function also as space-making cells. It is to be noted that they are binucleated as compared with the sterile cells in the caecoma and aecidium cup, but in their position and behavior they certainly agree with the sterile cells of the other forms. That these interesting cells may exist in the uredo- and teleuto-sori of other genera is probable and the problem as to their morphological nature calls for careful investigation. Galloway (21) discusses the development of the teleutosori in *Gallowaya Pini* as follows: "The upper cells of each sporophore give rise to a mass of gelatinous substance, which has no definite structure, so far as can be ascertained. It is the sudden development of these gelatinous masses that ruptures the cortical tissue, thus bringing the sorus into direct contact with the air, moisture and more intense sunlight". His description is further confirmed by Figs. 13 and 17, which are very suggestive that the cells shown are the equivalent of a buffer or sterile cell. Fisher (17) in his diagram of the teleutosorus of *Coleosporium Melampyri* (Fig. 299) shows a single row of empty cells overlying the teleutospores; as also Dietel (12) in his Figure 27 of *Coleosporium Euphrasiae*. In looking over some of my sections of sori in *Coleosporium delicatulum* and *C. solidaginis*, I have observed the same structures, which I consider the equivalent of sterile cells. So far as I can determine Kurssanow (28) was the first to give evidence for the fusion of gametes in the genus *Peridermium*. In Plate 6, Fig. 8 of *Peridermium Pini* (*Coleosporium*) he shows a two-legged basal cell. Fertilization in the five species of *Peridermium* that I have studied is effected by the fusion of two gametes of similar size and origin. There was no evidence of nuclear migrations such as were described by Blackman. Following the fusion of the two gametes there is a marked increase in the volume of the binucleate fusion cell, which later functions as the basal cell for a row of aecidiospores. The fusion cells are very easily found and the young primordia of *P. Comptoniae*, *P. verruciforme* and *P. aciculum* are particularly favorable forms to demonstrate this phenomenon.

The development of the peridium appears to be associated in these forms with an extensive development of pseudoparenchyma. The central arch of the peridium is composed of the apical metamorphosed aecidio-

spores of the inner spore chains, while the peripheral chains consist entirely of metamorphosed spores. Exception is found in the central arch of the aecidium of *P. Comptoniae*, where the peridium is two to four cells in thickness. The entire peridium that covers the aecidium is apparently for the protection of the enclosed spores. The peridial cells may be early recognized by their vacuolar cytoplasm, which eventually disappears. The change in the cytoplasm appears to be correlated with the thickening of the cell walls. The intercalary cells in the peripheral chains do not persist as long as those in the other chains, which, together with the fact that they are cut off from the lower outer edge of the initial spore-mother cell, may account for their having been overlooked except by Richards (36), Hoffman (26), Moreau (30), and Kurssanow (28), whose figures show them clearly.

Ludwig and Rees (29) have recently investigated the origin of the uredo-sorus in *Pucciniastrum agrimoniae*, a form which possesses a peridium. They observe that the "Apical cells of the columns elongate considerably and the protoplasmic contents became less dense, as is shown by a tendency to stain less deeply than at first. They are evidently the first peridial cells to be differentiated and the other cells of the chains are spores. No intercalary cells were seen and no chains were observed having more than three or four spores to the chain". Nothing is said regarding the persistency of the peridium, but otherwise it would agree in its origin and behavior with the regular peridial cells in the aecidium. The peridial cells in this case are metamorphosed spores as in the aecidium, but intercalary cells are wanting, since the peridial cell is a terminal metamorphosed spore of a chain originating from a binucleate mycelium. If this peridium is analogous to that of the aecidium, it is to be noted that it is not associated with any extensive development of pseudo-parenchyma as in the case in the forms I have studied.

The division of the peridial initial cells in the central arch of the aecidium of *Peridermium acicolum* cuts off an intercalary cell above. Kurssanow has already reported this condition in *Peridermium Pini*. Further investigations of the leaf forms may throw additional light on this condition.

The size of the aecidium in *P. acicolum*, *P. Paecki* and *P. bresenianum* is early determined by the breadth of the primordium. In *P. Comptoniae* and *P. pyriforme* the aecidia are unlimited in their development, the apparent determining factor being the food supply. This explanation also has been suggested for the caecoma. In this respect the type in these two

species is strikingly different from that of the aecidia hitherto studied. They resemble the caecoma in their indeterminate growth and the aecidium cup in their deep origin and the presence of a peridium.

SUMMARY

1. Sexual cell fusions and development of the aecidium were studied in five species of *Peridermium*, *P. Comptoniae*, *P. pyriforme*, *P. aciculum*, *P. Peckii* and *P. balsameum*.

2. In the two stem forms studied (*P. Comptoniae* and *P. pyriforme*) the spermogonia are a caecomoid type of fructification, being apparently unlimited in their development. These caecomoid spermogonia originate between the cork layer and cortical parenchyma and thus are to be considered cortical in origin and not sub-epidermal. They are irregular in outline and the margins are not delimited, but consist of a spreading plectenchyma or anlage. The spermogonial layer appears as a broad, flat crust-like layer with no definite aperture for the escape of the spermatia, which apparently depend for their escape upon the irregular cracking of the overlying tissue. They were observed developing in the tissue overlying the young aecidia as well as in the adjacent tissue.

3. The spermogonia in the leaf forms are early delimited. They are conoidal to hemispherical in outline and possess a definite aperture for the escape of the spermatia.

4. The gametophoric hyphae form a conspicuous palisade layer in the aecidial primordia of *P. Comptoniae*, *P. pyriforme*, and *P. aciculum*.

5. The pseudoparenchyma of the aecidial primordia is made up of the peripheral portions (sterile cells) of the gametophoric hyphae and is sharply defined from the fertile layer.

6. The sterile cells of the gametophoric hyphae are homologous to the so-called "buffer cells" of the caecoma.

7. Sexual cell fusions occur between adjacent fertile cells of similar size and position in two gametophoric hyphae. A dissolution of the walls occurs usually at the upper ends or where they come in contact. This phenomenon proceeds so as to result ultimately in the complete disappearance of the contact walls, thus forming a fusion cell.

8. The development of a peridium appears to be associated in these forms with an extensive development of pseudoparenchyma.

9. The central arch of the peridium is composed of the apical metamorphosed aecidiospores of the inner spore chains. An exception is found in the aecidium of *P. acicolum* where the division of the peridial initial cells in the central arch cuts off an intercalary cell above.

10. The lateral portion of the peridium consists entirely of metamorphosed spores.

11. In *P. Comptoniae* the central arch of the peridium is two to four cells in thickness.

12. The size of the aecidium in *P. acicolum*, *P. Peckii* and *P. balsameum* is early determined by the breadth of the primordium.

13. The aecidia of *P. Comptoniae* and *P. pyriforme* resemble the caeoma in their indeterminate growth and the aecidium cup in their deep origin and the presence of a peridium.

14. In *P. Comptoniae* and *P. pyriforme* the effect of the development of the spermogonia and aecidia is such as to kill the immediately adjacent tissue. This tissue is sloughed off in the late summer with the formation of a new cork layer.

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EXPLANATION OF PLATE 1

All figures were drawn with the aid of the camera lucida, and magnification noted with each description. They are shown as in their natural position in the sori with the top of the page representing the direction of growth towards the host epidermis.

Plate 1 Fig. 1. *Peridermium pyriforme*. Early stage of fusion. X 2040.

Fig. 2. *Peridermium Peckii*. Incomplete fusion cell. The two sterile cells above the gametes their protoplasm and are gradually pushed up with the others to make up the pseudoparenchyma and finally disorganize. Two sub-basal cells are shown below the gametes. X 2040.

Fig. 3. *Peridermium pyriforme*. Same as Fig. 1 showing seriation of the gametophoric hyphae. The sterile cells a, b, c and d are the lower cells of the right and left gametophoric hyphae. Only one sub-basal cell is shown below each gamete. X 2040.

Fig. 4 and 5. *Peridermium Comptoniae*. Completed fusions showing relation of the sterile cells (a, b, c, d) to their gametes and the sub-basal cells below. X 2040.

Fig. 6. *Peridermium pyriforme*. A multiple fusion between four fertile cells, two of which occur in the same chain. The bud-like outgrowth to the right is an upgrowth of the fusion cells. It is possible this would have resulted in a multi-nucleated basal cell such as have been found in *acidium* cups, as reported by other investigators. X 2040.

Figs. 7 and 8. *Peridermium pyriforme*. Two legged basal cells. X 2040.

Fig. 9. *Peridermium balsameum*. A completed fusion in which the nuclei have divided to form the daughter nuclei for the *acidiospore* initial cell. These have moved towards the upper part of the elongated basal cell before the initial cell is cut off. X 2040.

Fig. 10. *Peridermium aciculum*. A basal cell from the center of an *acidium* which has cut off its first *acidiospore* initial cell. This has further divided, cutting off an intercalary cell above. The spore below will become metamorphosed to form one of the central peridial cells. X 890.

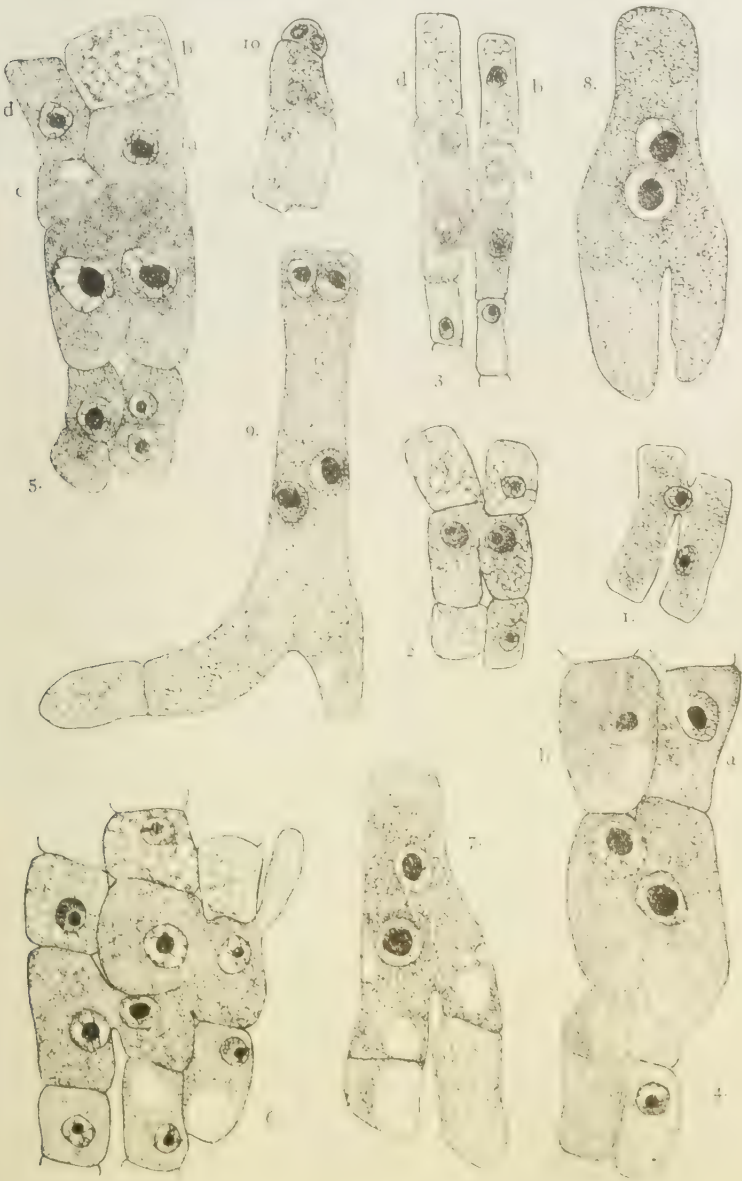


PLATE I.

EXPLANATION OF PLATE 2

Plate 2. Figs. 11 and 12. *Peridermium balsameum*. Two complete fusions showing basal cells below each gamete. X 2153.

Fig. 13. *Peridermium acicolum*. A completed fusion cell showing three sub-basal cells below. X 2153.

Fig. 14. *Peridermium acicolum*. Same as Plate 1, Fig. 10 showing two sub-basal cells below the gamete. X 1076.

Fig. 15. *Peridermium acicolum*. A young central chain. From below it shows a basal cell (b) which has cut off two aecidiospore initial cells. The first one has divided, cutting off an intercalary cell (i) above and the spore below has become metamorphosed to form the apical peridial cell (p). The initial cell below has divided but the intercalary cell (i) is cut off below the aecidiospore (s) in the usual way. X 987.

Fig. 16. *P. Comptoniae*, 17. *P. pyriforme*, 18. *P. acicolum*, 19. *P. Peckii* and 20. *P. balsameum*. Peripheral peridial chains showing method of development. The basal cells are shown from which are cut off the aecidiospore initial cells. As a rule the aecidiospore initial cells next to the youngest are the first to cut off the intercalary cells. The intercalary cells are cut off from the lower outer edge of the initial spore mother cell, thus making the peridial cells metamorphosed spores. The intercalary cells in the peripheral chains do not persist as long as those in the other chains. X 987.

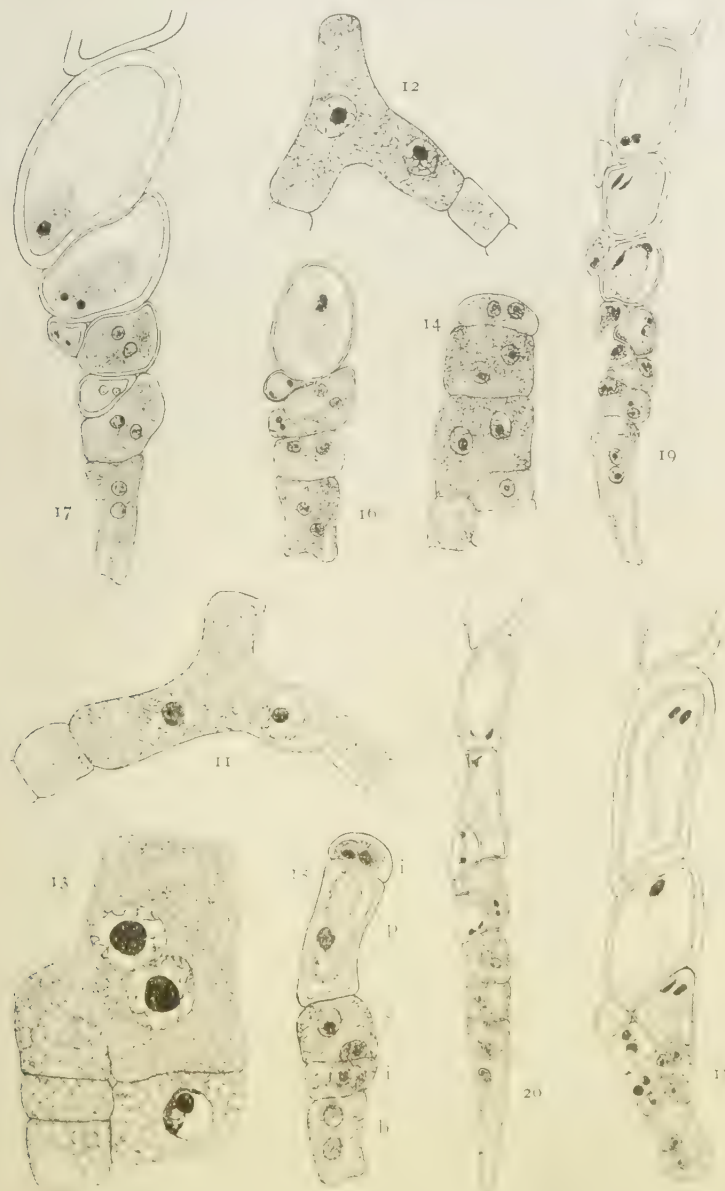


PLATE II.

EXPLANATION OF PLATE 3

Plate 3. *Peridermium Comptoniae*. Cross section through portion of aecidium. Only the adjacent host cells above and below the aecidium are shown. To the left of this figure the aecidium showed greater maturity, while to the right and extreme left the young advancing margins were present. In the portion of the aecidium drawn fusion has been completed and spore formation has progressed. Certain groups of fusion cells appear to be more precocious than others so that groups of basal cells produce a greater number of spore mother cells than others. This is shown by the uneven outline of the peridial layer which is represented by the double walled cells. In some cases all the first four acidiospores become metamorphosed into peridial cells. The central arch in this species is thus found to be made up of a layer of metamorphosed spores at least two to four cells in thickness. Above the peridial cells is the pseudoparenchyma which is pushed upward with the maturing aecidium and later becomes disorganized and disappears at maturity, the overlying host tissue gradually ruptures irregularly when the aecidium becomes exposed. The basal cells are indicated by their protoplasmic contents. Cp. cortical parenchyma, p. peridial cells, s. acidiospore, i. intercalary cells, a. acidiospore initial cells, b. basal cell, sb. sub-basal tissue. X 561.

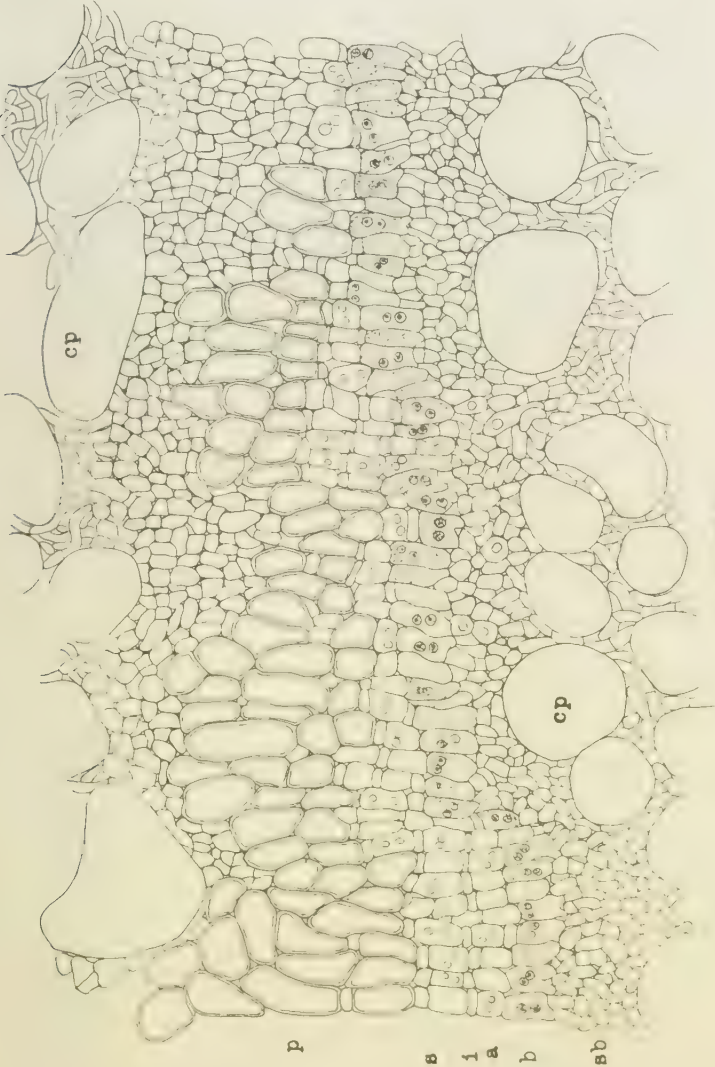


PLATE III.

EXPLANATION OF PLATE 4

Plate 4. *Peridermium pyriforme*. Section of young aecidium primordium drawn from a radial section. Further to the right of this section the aecidium showed progressively greater and greater maturity with fusion cells and basal cells that had cut off peridial cells as well as spores. On the left is the young advancing margin. The interlaced cells are rich in protoplasm as compared with the vegetative hyphae. The hyphae at this point in part grow towards the surface of the host as well as in the direction of the spreading primordium. On the right the gametophoric hyphae are more definitely oriented with their direction of growth entirely towards the surface. The cells making up these hyphae at this stage of maturity are shorter and thicker forming a distinct palisade layer. The apical cells of the gametophoric hyphae have not started to disorganize. Their protoplasmic contents and nuclei are intact. X 545.

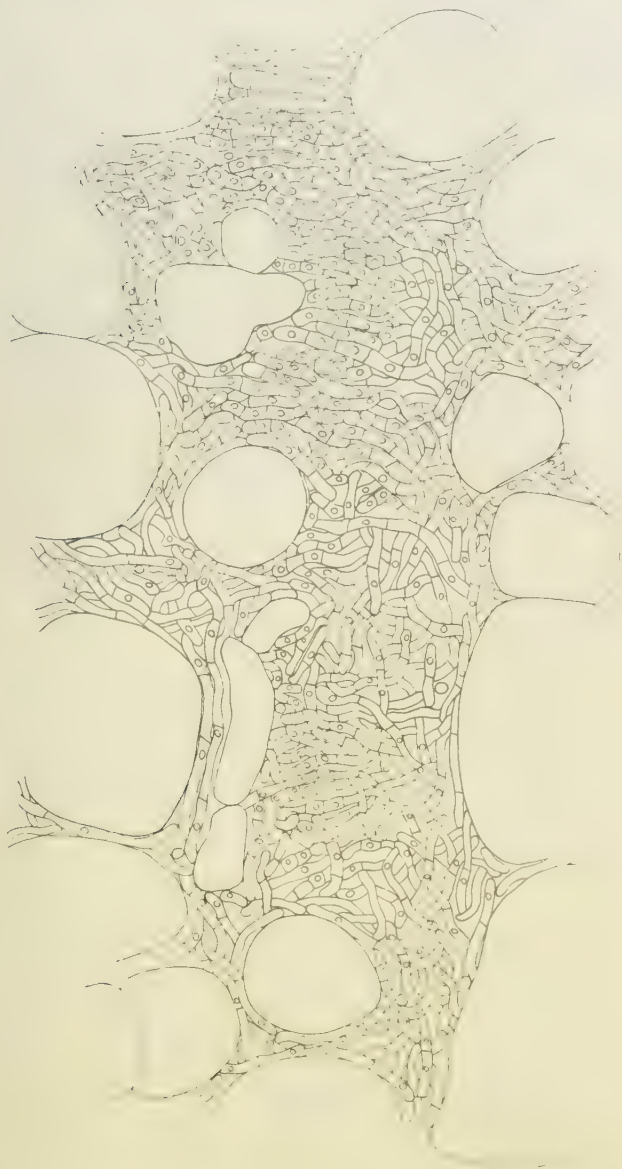


PLATE IV.

EXPLANATION OF PLATE 5

Plate 5. *Peridermium aciculum*. Portion of an acicidium primordium from cross section of leaf. The primordia originate between the palisade and hypodermal cells. The gametophytic hyphae form a definite palisade layer with their growth towards the leaf surface. The gametes or fertile cells are easily recognized by their deeply staining contents. Above the gametes are found the sterile cells which make up the pseudoparenchyma, and at this stage the cells contain little or no protoplasm. Fusion between the gametes proceeds from the center to the lateral margin of the acicillum. The large basal cells can be recognized in the central portion where they have cut off the first acidiopore initial cells. Fusion of the gametes in this primordium had not proceeded to the lateral margins. The pseudoparenchyma is pushed upwards following the production of spores and gradually disappears. The shallow sub-basal tissue is found to be made up of only two or three cells below the gametes. X 1000.

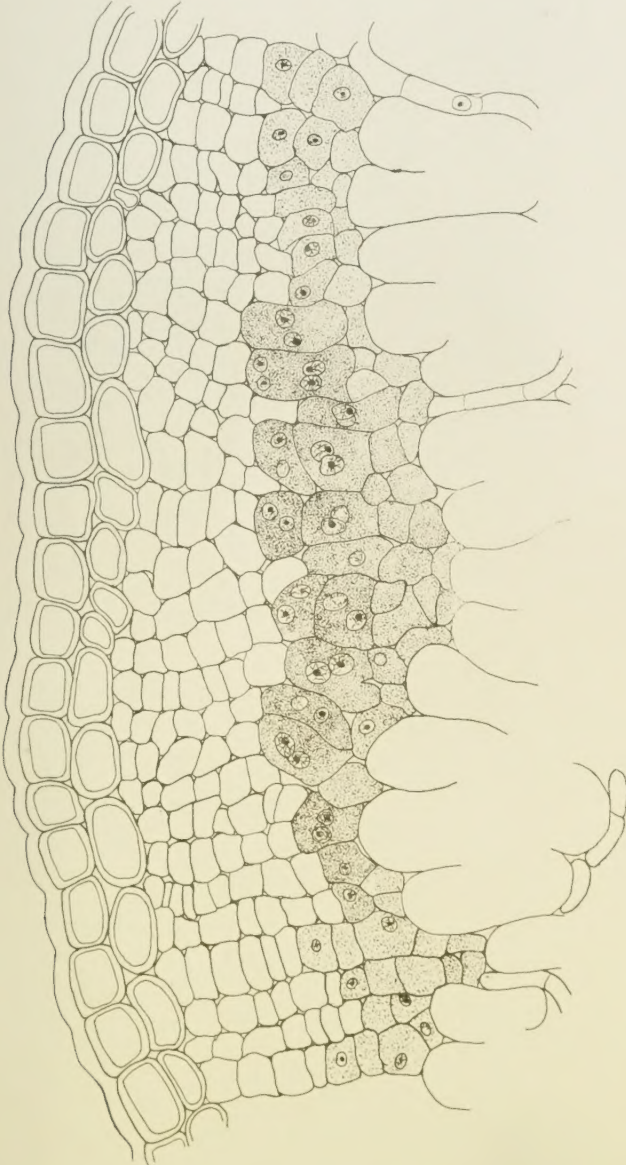


PLATE V.

